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Anatomy, Ontogeny, and Phylogeny of Coelophysoid Theropods

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Anatomy, Ontogeny, and Phylogeny of Coelophysoid Theropods

by

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"Go to nature - take the facts into your own hands - look, and see for yourself."

- L. Agassiz

(Quote adorning the front of the Ruthven Museums Building, the University of Michigan, Ann Arbor, Michigan.)

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Anatomy, Ontogeny, and Phylogeny of Coelophysoid Theropods

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Coelophysoid theropods (Dinosauria: Saurischia) were viewed as members of Ceratosauria in early cladistic phylogenetic hypotheses, but more recent analyses placed Coelophysoidea and *Dilophosaurus* as successively closer outgroups to Neotheropoda (Ceratosauria + Tetanurae). Most cladistic studies did not appreciate the importance of relative maturity to the expression of some characters in coelophysoids. Often the role played by ontogenetic variation was not considered, or maturity-dependent characters were deleted from analyses. I used cladistic techniques to derive a hierarchy of relative maturity and map the sequence of ontogenetic transformations among coelophysoid specimens. I then conducted an extensive phylogenetic analysis of basal theropod relationships. Taxa and characters used in the phylogenetic analysis were examined in

detail. Separate phylogenetic tests were run to evaluate different approaches to dealing with the relative maturity of specimens in cladistic analyses. The first test coded characters as if all taxa were represented by adults, and resulted in a taxon known only from immature specimens being placed in a basal position. The second test removed maturity-dependent characters from consideration, and resulted in Coelophysoidea being placed outside Ceratosauria, basal to Neotheropoda. The third test incorporated the results of the ontogenetic analysis. Maturity-dependent characters were coded as 'missing data' instead of 'absent' in taxa represented by immature specimens if the ontogenetic analysis showed the derived states of characters were expressed only at stages of maturity more advanced than the representative specimens. The third test resulted in Coelophysoidea being placed as the sister lineage to Ceratosauroidea within Ceratosauria. My study shows that the approach used to deal with ontogenetic variation in fossil taxa can alter the outcome of phylogenetic analyses. The use of a quantitative ontogenetic analysis to determine the relative maturity of fossil specimens, the subsequent approach to coding maturity-dependent characters for taxa represented by immature specimens, and the addition of new anatomical data all contributed to more robust hypotheses of relationships among basal Theropoda.

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INTRODUCTION

Theropods are attention-getters. For better or worse, theropod dinosaurs have been a focus of humanity's fascination with prehistory since the existence of long-extinct, giant reptiles was first recognized. Humans tend to hold large, powerful predators in special places of respect and fear, which may explain the continued popularity of these creatures in both public and professional eyes. The anatomy and relationships of theropod dinosaurs began to garner even greater attention from paleontologists in the early 1970s. This marked the beginning of a recent re-emergence of interest in dinosaurs. The renewed interest was ignited in part by fossil discoveries that resurrected long forgotten hypotheses of a close relationship between extinct dinosaurs and extant birds. The second wave of the dinosaur resurgence swept through the paleontological community in the mid-1980s, starting with the first serious application of cladistic methodology to saurischian phylogeny reconstruction (Gauthier, 1986).

The scientific attention given theropods was not shared equally across the entire clade. Most efforts focused on reconstructing the evolutionary history of coelurosaurian (Coelurosauria sensu Gauthier, 1986) theropods. This is understandable because Coelurosauria includes birds and the transitional forms leading to them. The fossil record of non-avian coelurosaurs is also relatively good, with many taxa and specimens known from sediments of Late Jurassic and Cretaceous age worldwide. The emphasis of research on coelurosaurian taxa resulted in few rigorous studies conducted on taxa and relationships near the base of the theropod lineage. This disparity was also propagated by

the relative scarcity of theropod fossils from rocks of Late Triassic through Middle Jurassic age, the time frame during which theropods (and other dinosaurs) appeared and began to diversify.

Gauthier (1986) provided a starting point for cladistic studies of theropod phylogeny, and was the first to recognize a basal split among theropods between those taxa more closely allied to birds (=Tetanurae), and those more closely related to the Late Jurassic taxon *Ceratosaurus nasicornis* (Fig. 1A). The latter was christened Ceratosauria (Gauthier, 1986; Rowe, 1989). Ceratosaur relationships were more fully investigated by Rowe (1989) and Rowe and Gauthier (1990). These authors suggested that several taxa of small to medium-sized, lightly built theropods from Late Triassic to Early Jurassic times were also ceratosaurs. Among them was the well known taxon *Coelophysis bauri*, and the lineage of ceratosaurs more closely related to *Coelophysis* than to *Ceratosaurus* was later coined Coelophysoidea (Holtz, 1994) (Fig. 1B).

Coelophysoids are the most abundant theropod fossils known from Late Triassic through Early Jurassic age sediments worldwide. Their remains are known from Africa (Raath, 1969, 1977, 1990), Europe (Fraas, 1913; Huene, 1934; Ostrom, 1981; Sereno and Wild, 1992), South America (Arcucci and Coria, 2003; see below), and Asia (Hu, 1993; Irmis, 2004). However, North American sediments produced the greatest record of coelophysoid diversity. Fragmentary remains with few diagnosable apomorphies are known from beds in eastern North America (Talbot, 1911; Colbert and Baird, 1958; Colbert, 1964a). Better and more numerous specimens come from the Colorado Plateau of Arizona and New Mexico, and also from the Dockum Group sediments of eastern New

Mexico (Cope, 1887, 1889; Camp, 1936; Welles, 1954, 1970, 1984; Colbert, 1964a, 1989; Parrish and Carpenter, 1986; Rowe, 1989; Long and Murry, 1995; Carpenter, 1997; Hunt et al., 1998; Heckert et al., 2000; Lucas and Heckert, 2001). Sediments of the Glen Canyon Group in northeastern Arizona produced several coelophysoid taxa, including *Segisaurus halli* (Camp, 1936), *Dilophosaurus wetherilli* (Welles, 1954, 1970, 1984), *"Syntarsus" kayentakatae* (Rowe, 1989; see Ivie et al., 2001), a taxon informally labeled the Shake-N-Bake theropod (Tykoski, 1997, 1998), and possibly an additional theropod from the Moenave Formation (Lucas and Heckert, 2001).

A major shift in the concept of Ceratosauria began after similarities were noticed between *Ceratosaurus* and members of the Abelisauridae, a group of large but poorly known theropods from Cretaceous deposits of Gondwanan landmasses (Novas, 1989a, 1992; Bonaparte et al., 1990; Bonaparte, 1991). Cladistic studies (Holtz, 1994, 1998; Rowe et al., 1997; Tykoski, 1998; Sereno 1999a) later supported the assertion that *Ceratosaurus* and abelisaurids constituted a sister-taxon to the coelophysoids (Novas, 1989a, 1992; Holtz, 1994, 1998; Sereno 1998, 1999a) (Fig. 1B). The name Neoceratosauria was erected by Novas (1992) and later defined phylogenetically for the clade comprising the most recent common ancestor of *Ceratosaurus* and Abelisauridae and all of its descendants (Holtz, 1994). The discovery of the basal theropod *Eoraptor lunensis*, and better material of the purported basal theropod *Herrerasaurus ischigualastensis* contributed important information to our knowledge of basal theropod evolution (Sereno et al., 1993; Novas, 1993; Sereno, 1993; Sereno and Novas, 1993). More detailed descriptions of basal dinosauriforms (Table 1) such as *Lagerpeton*

chanarensis and *Marasuchus lilloensis* also provided better outgroup selection for all cladistic studies on basal dinosaur systematics (Sereno and Arcucci, 1993, 1994).

The high degree of morphological dissimilarity between coelophysoids and neoceratosaurs caused some workers to question the monophyly of Ceratosauria, and competing hypotheses of basal theropod relationships were proposed (Rauhut, 1998, 2003; Carrano and Sampson, 1999; Forster, 1999; Sampson et al., 2001; Carrano et al., 2002). These studies found *Ceratosaurus* and the abelisaurids were more closely related to tetanuran theropods than to the coelophysoids, thereby excluding the coelophysoids from Ceratosauria (Fig. 1C; see taxonomy below). The analyses benefited from the cumulative increase in the number of characters examined in each cladistic analysis, as well as the discovery of new and better specimens of *Ceratosaurus* and abelisaurs. They eventually caused the momentum of opinion to swing towards the exclusion of coelophysoids from Ceratosauria.

Recent authors utilized a greater understanding of neoceratosaur anatomy in their analyses, but did not incorporate much new information concerning coelophysoid anatomy. New data come from specimens collected from exposures of the Kayenta Formation (Early Jurassic: Sinemurian-Pliensbachian) within the boundaries of the Navajo Nation of Arizona. A number of collecting seasons by crews from The University of Texas at Austin recovered a wealth of new specimens that formed much of the basis of my work.

No fewer than three coelophysoid taxa are represented by fossils from the Kayenta Formation, including the purportedly basal coelophysoid *Dilophosaurus*

wetherilli, the more derived taxon *"Syntarsus" kayentakatae*, and the Shake-N-Bake taxon. Many of the specimens preserve anatomical details that were unavailable to previous authors. Also, close re-examination of already known coelophysoid fossils revealed a wealth of phylogenetically informative morphology that was previously overlooked, misinterpreted, or was in need of revision given recent hypotheses of theropod evolution.

A critically important issue in phylogeny reconstruction of fossil vertebrates is the role ontogeny plays in the expression of morphology, and its effect on the interpretation of characters. The ceratosaur (either including or excluding Coelophysoidea) skeleton exhibits a high degree of co-ossification in parts of the skeleton, particularly in the pelvis, sacrum, and tarsus. The co-ossification of these elements is unusal among basal dinosaurs, although derived tetanuran clades convergently acquired many of these features later in Mesozoic time. Most previous cladistic analyses of basal theropod relationships recognized at least some of these features as phylogenetically informative, (Gauthier, 1986; Rowe, 1989; Rowe and Gauthier, 1990; Holtz, 1994, 1998; Sereno, 1999a; Carrano et al., 2002), but none of them explicitly addressed the effect of scoring maturity-dependent characters in taxa known only from immature specimens. One author recently argued that osteological fusions were uninformative in cladistic analyses of basal theropods, and removed these characters from consideration (Rauhut, 2003).

The goal of my work is to obtain a more robust hypothesis of basal theropod relationships, with an emphasis on the position of Coelophysoidea. I bring a great deal of new anatomical information and interpretation to bear on the issue, mostly derived from

first-hand examination of specimens from the Kayenta Formation. I directly address the issue of ontogeny estimation by use of a technique to determine the relative ontogenetic status of individual specimens, and then score taxa appropriately in a cladistic analysis. The issue of ontogenetic state assessment is dealt with first, followed by an extensive phylogenetic analysis of basal theropods. I enter into this work with no desired outcome other than finding the best-supported hypothesis of phylogeny given the morphological and ontogenetic data available. A list of the anatomical abbreviations used throughout this work is given in Appendix 1.

Taxonomy

It is important that explicit definitions be established for the names of clades. I recognize the validity of clade names based upon their first stable, ancestry-based definition in most cases. In other words, the first published node-based or stem-based name definition for a clade is recognized whenever possible (Padian and May, 1993), except in some instances where there is a great discrepancy between the original intent of the coining author and subsequent taxonomic content. There are instances where otherwise legitimate ancestry-based definitions are known for given clades, but the phylogenetic position of the reference taxa upon which the names were based is uncertain (e.g., Ceratosauria sensu Sereno, 1998). This resulted in instability of the definition and caused conflicts with other, firmly established taxonomic definitions. In such cases I reject the unstable definition in favor of the next most recent, stable, ancestry-based definition. Table 1 lists the taxonomic names and definitions used throughout my work.

Figure 2 depicts of the relevant clade names and definitions on the two main competing hypotheses of basal theropod phylogeny. A review of theropod taxonomy was presented by Padian et al. (1999), and many of their recommendations are applied here.

Ceratosaurian taxonomy was complicated by less-than-explicit definitions supplied when the names were first erected (Gauthier, 1986; Novas, 1992; Holtz, 1994). This caused ambiguity in the taxonomic content of clades and prompted some authors to openly avoid the issue (Carrano et al., 2002). The primary reason for the ambiguity was that the names were erected during the early days of cladistic methodology in vertebrate paleontology and the use of ancestry-based definitions in taxonomy was still in its infancy. Given these caveats, the first stable ancestry-based definition for Ceratosauria was given by Rowe (1989:132), who in clarification of the names Tetanurae and Ceratosauria stated, "Tetanurae includes those theropods more closely related to birds (and includes birds), whereas Ceratosauria includes taxa more closely related to *Ceratosaurus nasicornis*." The format of this definition did not exactly match most given in recent years, but it clearly met the requirements of being ancestry-based (a stem-based definition in this case), and it identified two reference taxa (contra Wilson et al., 2003) upon which the name was anchored (*Ceratosaurus nasicornis* and 'birds'). The only potential complaint could be that the content of 'birds' was not explicit. However, it is inconsequential whether 'birds' as envisioned by Rowe (1989) was meant to include Aves sensu Gauthier (1986), Aves sensu Padian et al. (1999), Neornithes sensu Sereno (1998), or *Gallus gallus*. The name Ceratosauria was later given a node-based definition by Rowe and Gauthier (1990). Later works (Holtz, 1994; 1998; Rowe et al., 1997; Sereno,

1997, 1998, 1999a; Carrano et al., 2002; Wilson et al., 2003; Sereno et al., 2004) continued to use Ceratosauria in the stem-lineage sense, and I follow suit here.

The effort by Sereno (1998) to offer ancestry-based names for dinosaurian clades was commendable but suffered some drawbacks. Some taxa used as reference taxa were known from very incomplete specimens, and their phylogenetic position relative to other taxa was uncertain. In addition, many clade names and definitions that were already established and in common use were not recognized. This had negative effects upon taxonomic stability and the ease of communication between theropod researchers. This was especially the case with ceratosaur clade names, with the result that the taxonomic definitions offered by Sereno (1998) contributed in part to claims that Ceratosauria was paraphyletic (Carrano and Sampson, 1999; Sampson et al., 2001; Carrano et al., 2002). Much of the taxonomic revision proposed by Sereno (1998) was recently expanded upon by Wilson et al. (2003). The taxonomic revisions offered by Wilson et al. (2003) were extensive, with many established clade names and definitions overturned and altered. Taxonomic destabilization and confusion among theropod systematists may result if several of the taxonomic revisions proposed by Wilson et al. (2003) are adopted.

The name Neotheropoda was not formally diagnosed at the time it was first applied (Bakker, 1986), a fact correctly pointed out by Wilson et al. (2003). It is clear from the diagram in which Neotheropoda was first used that the author intended the name to encompass *Ceratosaurus* and those theropods leading to the avian clades, to the exclusion of *Coelophysis* and its closest kin (Bakker, 1986). This sentiment was followed by Holtz (1998) and Padian et al. (1999) who chose *Ceratosaurus* and

Neornithes (=Aves sensu Gauthier, 1986) as reference taxa for a node-defined Neotheropoda. The spirit of the taxonomic content of the name was not followed by Sereno (1998) and Wilson et al. (2003) who expanded the taxonomic content of the clade by selecting *Coelophysis* and Neornithes as reference taxa for the node-defined clade Neotheropoda. The use of *Coelophysis* instead of *Ceratosaurus* as a reference taxon for Neotheropoda has the potential to contradict the original taxonomic intent of the name in phylogenetic hypotheses that find coelophysoids are an outgroup to a Ceratosauria + Tetanurae clade. I therefore use the definition of the name adopted by Holtz (1998) and Padian et al. (1999).

The name Ceratosauroidea was phylogenetically defined as all theropods more closely related to *Carnotaurus* than to *Coelophysis* (Sereno, 1998). The content of the name may be equivalent to the name Neoceratosauria as conceived by Novas (1992), and it is certainly equivalent to the name Neoceratosauria as used by Holtz (1998) and Padian et al. (1999). This point was highlighted by Wilson et al. (2003), who argued against using Ceratosauroidea or Neoceratosauria. Their arguments centered on the fact that as defined, the name Ceratosauroidea or Neoceratosauria would apply to the stem lineage that includes Ceratosauria and Tetanurae in hypotheses of theropod phylogeny that place Coelophysoidea as an outgroup to the Ceratosauria + Tetanurae clade.

The reasons offered by Wilson et al. (2003) to justify abandoning both names were not well founded. They did not recognize the name Ceratosauroidea because it would be, "an inappropriate name to apply to this node because its Linnean rank is equal to or below many of the groups it supposedly includes" (Wilson et al., 2003:29). They

argued against use of the name Neoceratosauria because the etymology of the name ("new Ceratosauria"), "suggests that it should refer to a subclade of Ceratosauria" (Wilson et al., 2003:29). There is no explicit reason why the Linnean rank of a clade name should determine whether a name is "inappropriate" as defined and applied in phylogenetic taxonomy. I recognize the name Ceratosauroidea as phylogenetically defined by Sereno (1998), which encompasses the sister stem-lineage to Coelophysoidea either within Ceratosauria (Fig. 2A), or encompassing Ceratosauria and Tetanurae (Fig. 2B). Given the advocacy of node-stem triplet use by Sereno (1998) and Wilson et al. (2003), it should be desirable that this sister lineage to Coelophysoidea carry an explicit name.

Neoceratosauria was not clearly defined as either a node- or a stem-clade name by Novas (1992). The first explicit, ancestry-based definition for the name was, "the group composed of the most recent common ancestor of *Ceratosaurus* and Abelisauridae and all of its descendants" (Holtz, 1994:1104). This is an unambiguous node-based definition of Neoceratosauria, a fact pointed out by Sereno (1999b). Neoceratosauria was later given a stem-based definition, with Holtz (1994) incorrectly cited as the source for the stem-defined name (Holtz, 1998; Padian et al., 1999). The name was subsequently used in the context of a stem-lineage by several authors (Tykoski, 1998; Holtz, 1998; Padian et al., 1999; Carrano et al., 2002; Wilson et al., 2003; Tykoski and Rowe, 2004).

The use of a stem-definition for the name Neoceratosauria was based upon an error. I follow priority of the ancestry-based definition and use Neoceratosauria as the node-based clade name encompassing *Ceratosaurus* and *Carnotaurus* (instead of

Abelisauridae) and all descendents of their most recent common ancestor, as originally defined (Holtz, 1994) (Fig. 2A, 2B). The arguments offered by Wilson et al. (2003) for abandoning the name do not apply when Neoceratosauria is applied as a node-defined name as originally envisioned and defined by Holtz (1994).

I apply the name Abelisauria (Novas, 1992, 1997) to the node representing the most recent common ancestor of *Noasaurus* and *Carnotaurus* and all of its descendents (Fig. 2; Table 1). Abelisauroidea (Bonaparte, 1991) was defined phylogenetically by Holtz (1994) and applied to the stem lineage of all theropods closer to *Carnotaurus* than to *Ceratosaurus* (Holtz, 1994) (Table 1). The name Abelisauroidea was recently applied by Wilson et al. (2003) to the same node-based clade that already bore the name Abelisauria (Novas, 1997) (Table 1). It was argued (Wilson et al., 2003) that the original content of the name Abelisauroidea as envisioned by Bonaparte (1991) had been over-broadened by the subsequent use of the name applied to a stem-lineage. There was no explicit restriction of the taxonomic content of the name as originally coined by Bonaparte (1991), and it was not defined in an ancestry-based context. I therefore follow the principle of priority in recognizing the name Abelisauroidea as a stem-defined lineage (Holtz, 1994), and the name Abelisauria as a node-defined clade name (Novas, 1997) (Fig. 2; Table 1).

Relationships among the abelisauroids more derived than Noasauridae (sensu Wilson et al., 2003; Table 1) are not fully resolved because of the incompleteness of many of the pertinent taxa. The name Abelisauridae (Bonaparte and Novas, 1985) was defined by Novas (1997) to label the node encompassing *Abelisaurus comahuensis,*

Carnotaurus sastrei, *Xenotarsosaurus bonapartei*, *Indosaurus matleyi*, *Indosuchus raptorius*, and *Majungasaurus crenatissimus* and all descendents of their most recent common ancestor. Providing more than two reference taxa in the definition of an ancestry based clade name has the potential to result in taxonomic instability if hypotheses of relationships later indicate the exclusion of one or more of the multiple reference taxa from the originally conceived clade. An ancestry-based name is more stable if only two reference taxa are used to anchor its definition (de Queiroz and Gauthier, 1992; Sereno, 1998). Of the six taxa cited by Novas (1997) in his definition of Abelisauridae, four of them (*Xenotarsosaurus*, *Indosaurus*, *Indosuchus*, *Majungasaurus*) are based upon fragmentary remains that exhibit few diagnostic apomorphies, and are of uncertain phylogenetic position.

The name Abelisauridae was defined by Rowe et al. (1997) as the stem-lineage including all theropods more closely related to *Carnotaurus* than to *Elaphrosaurus*. The phylogenetic position of *Elaphrosaurus* proved to be variable relative to other ceratosauroids (Tykoski, 1998; Carrano et al., 2002; Rauhut, 2003), rendering the taxonomic content of the stem-name Abelisauridae unstable. A stable, ancestry-based definition for the name Abelisauridae was first provided by Sereno (1998), for the node consisting of *Abelisaurus*, *Carnotaurus,* and all descendents of their most recent common ancestor (Table 1). The same definition was adopted by Padian et al. (1999). This node-based definition is in the spirit of that originally conceived by Novas (1997), but more stable.

A stem-based definition for the name Abelisauridae was recently resurrected by Wilson et al. (2003), who based it upon a definition provided by Rowe et al. (1997). *Elaphrosaurus* was dropped as a reference taxon, and the name was re-defined to instead encompass those theropods more closely related to *Carnotaurus* than to *Noasaurus* (Wilson et al., 2003). It was argued that a stem-defined Abelisauridae represented an ideal sister taxon to the stem-defined clade Noasauridae (Wilson et al., 2003) in a node-stem triplet (sensu Sereno, 1998), and was therefore more desirable than a node-definition for the name. It may be advantageous to erect a stem-based name for the lineage of abelisauroids more closely related to *Carnotaurus* than *Noasaurus*. However, the name Abelisauridae already had a stable node-based definition (Sereno, 1998; Tykoski, 1998; Holtz, 1998; Padian et al., 1999; Carrano et al, 2002; Rauhut, 2003; Tykoski and Rowe, 2004). Changing the established meaning of the name could create taxonomic confusion, and violates the principle of priority. I therefore recognize the node-based definition of Abelisauridae provided by Sereno (1998), and not the stem-definition of Wilson et al. (2003).

I do not recognize the names Coelophysinae sensu Sereno (1998, 1999a, 1999b), or Procompsognathinae sensu Sereno (1998, 1999a, 1999b). The reference taxa used to anchor these names were *Coelophysis bauri* and *Procompsognathus triassicus*. The phylogenetic position of *Procompsognathus* among other coelophysoids was uncertain in my preliminary phylogenetic analyses (see Chapter 2), contrary to the phylogenetic hypothesis of Sereno (1997, 1998, 1999a). The contents of the clade names

"Coelophysinae" and "Procompsognathinae" as defined are therefore unstable, so I avoid them.

Most dinosaur clades with names erected prior to the advent of phylogeny-based taxonomy now have clearly defined names based upon ancestor-descendent relationships. These include most of the traditional names used in the literature for decades (i.e., Dinosauria, Saurischia, Theropoda; Table 1). This reflects the utility of the method of phylogenetic taxonomy proposed and advocated by de Queiroz and Gauthier (1990, 1992). It was recently argued (Rauhut, 2003) that the stability possible in phylogenetic taxonomy is somehow undesirable, an idea apparently taken from Dominguez and Wheeler (1997). Review of the latter work reveals a basic disconnect between the concept of nomenclatural stablity with respect to ancestry (phylogenetic taxonomy) versus stability with respect to characters (non-phylogenetic taxonomy).

It was correctly pointed out (Rauhut, 2003) that contradictory taxonomies were published by Sereno (1998) and Padian et al. (1999), and that instability was caused by Sereno's (1998) use of *Coelophysis* instead of *Ceratosaurus* as a reference taxon in defining the name Ceratosauria. The practice of not recognizing previously published ancestry-based definitions of clade names, and the use of reference taxa represented by inadequate specimens, must be viewed separately from the method of phylogenetic taxonomy itself. The problem of competing taxonomies is avoidable if authors respect and follow the principle of priority, and recognize the first node- or stem-based definition of a clade name based upon stable reference taxa.

Special attention must be given to the taxonomic status of the coelophysoid theropod *Syntarsus*. *Syntarsus rhodesiensis* is one of the best-known coelophysoids, with multiple specimens sampled across a wide range of ontogenetic stages. The anatomy of the taxon was described at length by Raath (1969, 1977, 1985, 1990), but there has been no recent re-evaluation of the osteology of the taxon. The similarity between the skeletons of *Syntarsus rhodesiensis* and material collected from the Kayenta Formation in the late 1970s was noted by Rowe (1989), who decided the material from Arizona shared two features with the African taxon that excluded either from assignment to *Coelophysis*. There was enough similarity between the Kayenta form and the African taxon that Rowe (1989) assigned the former to a separate species of *Syntarsus*, *S. kayentakatae*.

The 'congeneric' status of these two taxa subsequently went unquestioned, with one or two notable exceptions. Using gradistic arguments, Paul (1988, 1993) proposed that *Coelophysis bauri*, *Syntarsus rhodesiensis*, and *"Syntarsus" kayentakatae* were too similar to warrant generic differentiation, and considered all three to be species of *Coelophysis*. No rigorous character-based analysis was conducted to support Paul's conclusion. It was recognized (Paul, 1993) that some points of anatomy used to differentiate *Coelophysis* from *Syntarsus* were the result of incorrect reconstructions or misinterpretation of disarticulated material. These included the presence of nasal fenestrae in *Syntarsus* (doubtful), and the fact that some specimens of *Coelophysis* also exhibit fusion between the proximal ends of metatarsals II and III. These features were identified again by Downs (2000), who reiterated the lack of differentiation between well-prepared and preserved *Coelophysis* material and the published osteology of

Syntarsus rhodesiensis. Other characters cited by Paul (1993) as evidence for the synonymy of *Coelophysis* and *Syntarsus* are plesiomorphic for various coelophysoid or ceratosaur clades, and are not useful for grouping the three pertinent species under a single primary nomen (="genus" under rank-based taxonomy). The possibility that *Coelophysis bauri* and *Syntarsus rhodesiensis* were closer to one another than either was to *"Syntarsus" kayentakatae* was suggested by Paul (1993). That relationship is upheld here by my cladistic analysis.

The taxon *Syntarsus* was used as a single operational taxonomic unit (OTU) in multiple cladistic analyses with few questioning the sister-taxon status of the two species. As explained above, the presence of a shared primary nomen between taxa bears considerable weight, and it is easy for subsequent authors to assume there is considerable support for assigning species to the same primary nomen. However, this also tends to discourage subsequent workers from critically examining the actual relationships between species with a shared primary nomen. Phylogenetically informative differences between taxa can be ignored or lost in analyses as a result, and the likelihood of recovering an accurate hypothesis of phylogeny is diminished.

My analysis (Chapters 2 and 3) is the first cladistic, character-based analysis to treat the two putative species of *Syntarsus* as separate OTUs since that of Rowe (1989) and Rowe and Gauthier (1990). My results do not support the sister-taxon relationship between *Syntarsus rhodesiensis* and *"Syntarsus" kayentakatae*. Instead, a sister-taxon relationship between *Syntarsus rhodesiensis* and *Coelophysis bauri* is recovered, a result reminiscent of that reached by Paul (1993). *"Syntarsus" kayentakatae* is found to be

closer to *Segisaurus halli* than to either *Syntarsus rhodesiensis* or *Coelophysis bauri*. Removal of *Segisaurus* from the analysis results in *"Syntarsus" kayentakatae* taking the position of the proximal outgroup to a *Coelophysis* + *Syntarsus rhodesiensis* clade.

There are cases where biologists widely recognize the paraphyly of a 'genus' name, yet willingly accept the continued use of the name because of a long history of usage, the desire for clarity in communication, and because of the lack of resolution among species-level relationships (e.g., *Bufo*, *Hyla*, *Microtus*). It must also be acknowledged that a shared primary name implies relationship in human thought processes, even though there is no actual reason why a shared primary name necessarily requires relationship in a binomial taxonomic system. *"Syntarsus" kayentakatae* and *Syntarsus rhodesiensis* are the names applied to distinct, diagnosable taxa. If an insect, a beetle for example, were named "*Syntarsus smithi*", there is virtually no chance that any competent biologist would mistakenly assume a close, sister-taxon relationship between the dinosaur *Syntarsus rhodesiensis* and the beetle "*Syntarsus smithi*". The binomial construction of the species name clearly demonstrates the uniqueness of each taxon. Its diagnosis among a nested hierarchy of clades supports the place of each taxon among its close relatives to the exclusion of other very distantly related taxa with which it may share a primary name.

For better or worse, human nature does not easily allow the use of a shared primary name without a degree of implied relationship. The taxonomic system erected by Linnæi (1758) recognized this part of human nature, and post-Darwinian biologists continued to operate under the understanding that a shared primary name also implied

shared ancestry or relationship. Until the revision or replacement of the International Code of Zoological Nomenclature is finalized biologists must continue to operate under at least some of the conventions inherent in the code, preferably without causing additional future confusion in taxonomy.

The primary name *Syntarsus* should be replaced with regard to *"Syntarsus" kayentakatae*. It implies a sister taxon relationship between *Syntarsus rhodesiensis* and *"Syntarsus" kayentakatae* that is incorrect given the results of my analysis. Treating these two taxa as a single OTU had a negative impact on the ability of earlier analyses to obtain accurate hypotheses of basal theropod relationships. I enclose the name *Syntarsus* in quotation marks in reference to *"Syntarsus" kayentakatae* throughout my work, to highlight the fact that it is phylogenetically distinct from *Syntarsus rhodesiensis*, that the two taxa bear no sister-taxon relationship, and that a new primary name should be applied to *"Syntarsus" kayentakatae*. I also use the full binomial name for both taxa to explicitly identify which one of the two taxa is being discussed. A work to revise the taxonomy of the Arizona species is forthcoming.

It was recently revealed that the name *Syntarsus* had been previously applied to a zopherid beetle from Madagascar (Fairmaire, 1869). The entomologists who uncovered this discrepancy took it upon themselves to offer a replacement name for the theropod ("*Megapnosaurus*"), and published their revision in a venue rarely frequented by members in the field of vertebrate paleontology (Ivie et al., 2001). The primary author of the revisionist paper eventually notified members of the paleontological community via electronic communication on a number of internet discussion-groups and similar outlets.

The author quickly drew a considerable amount of fire from the vertebrate paleontology community. The general feeling was that parts of the International Code on Zoological Nomenclature Code of Ethics were violated by the actions of the authors involved (International Commission on Zoological Nomenclature, 1999). The revisionist authors failed to make a serious attempt to contact the still-active author who had applied the name *Syntarsus* to the theropod dinosaur (Raath, 1969), so as to give him a chance to replace the name himself. This professional courtesy is spelled out in the guidelines and recommendations of the International Code on Zoological Nomenclature. The replacement name was also viewed as flippant in nature by many paleontologists (*Megapnosaurus* = 'big dead lizard'), a practiced cautioned against in the International Code on Zoological Nomenclature. Many paleontologists also viewed the periodical in which the replacement name was published as an inappropriate venue (an entomological journal) for notifying the paleontological community of the change.

The International Code on Zoological Nomenclature Code of Ethics (International Commission on Zoological Nomenclature, 1999:124) states, "Editors and others responsible for the publication of zoological papers should avoid publishing any material which appears to them to contain a breach of the above principles." The actions of Ivie et al. (2001) probably qualify as examples of at least two and perhaps three breaches of the ethical principles spelled out in the ICZN Code of Ethics. The name "*Megapnosaurus*" was not used by Tykoski et al. (2002) in a paper published in *Journal of Vertebrate Paleontology*, one of the flagship journals of the vertebrate paleontology profession. This was well after news of the replacement name circulated in the paleontological

community. The name was also not used by Tykoski and Rowe (2004) in the second edition of *The Dinosauria* (Weishampel et al., 2004). If the success and longevity of the first edition of *The Dinosauria* (Weishampel et al., 1990) is any indication, the new edition of this volume will be a major reference and guide to vertebrate paleontologists for a number of years to come.

I continue to use the name *Syntarsus* in reference to the coelophysoid theropod throughout my work. The need to erect a new primary name for *"Syntarsus" kayentakatae* is also a consideration. The application of "*Megapnosaurus*" to this taxon would do little more than create a proliferation of synonymies for future paleontologists to disentangle. I choose to avoid passing that burden and potential confusion to future workers.

Institutional/Museum abbreviations:

AMNH, American Museum of Natural History, New York, New York

CMNH, Cleveland Museum of Natural History, Cleveland, Ohio

FMNH, Field Museum of Natural History, Chicago, Illinois

GPIT, Geologisch-Paläontologisches Institut der Universität Tübingen, Tübingen, Germany

MACN-CH, Museo Argentino de Ciencias Naturales, Colección Chubut, Buenos Aires, Argentina

MB, Museum für Naturkunde, Berlin, Germany

MCF-PVPH, Museo Municipal Carmen Funes, Paleontología de Vertebrados, Plaza Huincul, Argentina

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

MNA, Museum of Northern Arizona, Flagstaff, Arizona

NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico

PVL, Fundación "Miguel Lillo", San Miguel de Tucumán, Argentina

PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina

QG, originally catalogued at the Queen Victoria Museum, Harare (formerly Salisbury), now curated at the National Museum of Natural History, Bulawayo, Zimbabwe

SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany

TMM, Texas Memorial Museum, Austin, Texas

UA, Université d'Antananarivo, Antananarivo, Madagascar

UCMP, University of California Museum of Paleontology, Berkeley, California

UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Argentina

USNM, United States National Museum, Smithsonian Institution, Washington D. C.

UUVP, Utah Museum of Natural History, University of Utah, Salt Lake City, Utah

YPM, Yale Peabody Museum, New Haven, Connecticut

CHAPTER 1

Ontogenetic Stage Estimation of Coelophysoid Theropods

The practice of estimating the ontogenetic stage represented by individual fossil tetrapods is inexact and rarely performed. Zoologists who work upon extant organisms have the ability to directly observe the ontogeny of individuals, or they can sample mutiple individuals of a taxon at selected times in their ontogeny. Paleontologists are impeded relative to zoologists because they can never directly observe the ontogeny of an individual, nor can they choose the ontogenetic timing of samples taken from a population of a taxon. In spite of this, some efforts were made to at least find means to identify and categorize approximate, if arbitrary, stages of fossil vertebrate development (Bennet, 1983; Brinkman, 1988; Brochu, 1992, 1996; Sampson, 1993; Carr, 1999).

It is important to recognize and appreciate the ontogenetic status represented by individual fossil specimens. Failure to account for ontogeny can result in a false proliferation of taxa, with juveniles or sub-adults being mistakenly labeled "species" distinct from those based upon adult specimens of the same taxon. Adults of taxa originally based only upon juvenile or sub-adult material may also be mistaken for new taxa. Diminutive new taxa can be mistaken for juveniles of larger, previously known taxa (Tykoski, 1998). These scenarios can lead to taxonomic confusion. They can also misrepresent the faunal diversity present in a given paleoenvironent by either increasing or decreasing the apparent number of taxa known from a given interval in the fossil record.

Reconstructions of character development and evolution also can be affected adversely by failure to address the role of ontogeny in morphological expression. Reconstructing the evolutionary history of morphological modification through the history of a lineage can suffer if the given morphological structure is best expressed, or only expressed, at late stages of ontogeny. An example of this may be the expression of pneumatic features in the craniofacial and cervical regions of saurischians. It was suggested that pneumatizing epithelia in the craniofacial region of theropods played an active role in the excavation of osteological structures and cavities such as the promaxillary recess and fenestra, maxillary antrum and fenestra, and pneumatic excavations in the ascending process of the maxilla (Witmer, 1997). As such, it would be expected that features such as depth and degree of finishing of the bone rimming the antorbital cavity would be higher in older individuals than in younger. There would also be a greater propensity for variation and remodeling in the antorbital region because pneumatic diverticulae had more time to work upon the osseous tissues adjacent to them. This pattern was reported in tyrannosaurids (Carr, 1999). Little additional work along these lines has been pursued in other taxa, in part because of the difficulty in seeing many of these potentially pneumatic spaces in a non-destructive manner.

The most profound effect of not recognizing the ontogenetic stage preserved in fossil specimens is the possible influence upon phylogeny reconstruction. The impact of basing phylogenetic characters on the pattern of pleurocoel development in sauropod taxa known only from juvenile specimens was noted by Wedel (2003). The taxon *Pleurocoelus nanus* was cited as the epitome of this issue, because the type specimen is

an incomplete juvenile individual as suggested by the lack of neurocentral co-ossification and the weakly developed lateral pleurocoels in the cervical vertebrae. The taxon continues to be troublesome in phylogeny reconstruction and studies of the evolution of sauropod dinosaurs (Wedel, 2003).

Ontogeny and Ceratosauria

What role does ontogeny estimation have in studies of ceratosaurian phylogeny? The first cladistic studies of ceratosaur relationships were conducted by Rowe (1989), and Rowe and Gauthier (1990). Both works used a number of maturity-dependent characters in their analyses. Most of these maturity-dependent characters were expressed as fusions in the sacrum, pelvis, metatarsus, and between the tibia and tarsus. Another character was related to the dimorphism present in the proximal femur of at least some coelophysoid theropods. Many of these characters were cited in those works as diagnostic of Ceratosauria, increasing their importance to claims that the clade was monophyletic and included the coelophysoid theropods. Most subsequent studies that included ceratosaurs as an OTU utilized at least some of these characters even as character lists grew in number and complexity (Holtz, 1994, 1998; Tykoski, 1998; Forster, 1999; Sereno, 1999a; Carrano et al., 2002; Rauhut, 2003).

Four ontogenetic stages with the potential to be preserved as fossils were identified by Rowe and Gauthier (1990), recognized primarily by the degree of suture and fusion between postcranial elements. These were embryos, juveniles, sub-adults, and adults. Embryos were restricted to prehatchling specimens, unknown for ceratosaurs.

Juveniles included hatchlings to near full-grown individuals. Sub-adults were described as being of near maximum size but lacking signs that growth had ceased. They recognized adulthood in a specimen by the presence of fused axial intercentrum and atlantal centrum and fusion of the resulting structure to the axial centrum, fused scapulocoracoids, fused sacral and pelvic elements, and neural arches fused to the vertebral centra.

The establishment of arbitrary ontogenetic stages among ceratosaurs provided a framework for later workers to address ontogeny and its impact on phylogeny reconstruction. Nearly all the known specimens of *Dilophosaurus wetherilli* and *Liliensternus liliensterni* were sub-adult or juvenile individuals, a fact pointed out by Rowe and Gauthier (1990). Surprisingly, many subsequent studies did not modify the way in which these taxa were treated in character state coding, even though it was sometimes acknowledged there were questions about the relative maturity level of the specimens (Holtz, 1998; Carrano et al., 2002; Rauhut, 2003).

What are the possible consequences of not altering the treatment and scoring of such material? First, some taxa might not be represented by individuals of relatively late ontogenetic stage. Treating such specimens as if they were adults could result in undeveloped (or under-developed) morphologies being assessed for maturity-dependent characters that are expressed only in later stages of life. In other words, a character expressed only late in ontogeny could be coded as unambiguously 'absent' in a taxon known only from juvenile or sub-adult material. The danger is that an adult specimen of

the same taxon may actually possess the character, thereby altering the outcome of a cladistic phylogenetic analysis.

Second, proportional differences between very young and fully mature individuals could also have a negative impact on phylogeny reconstruction. Characters erected as part of a continuous morphological spectrum, or that compared an element's size relative to another skeletal component could be substantially affected by proportional changes in the skeleton that occur through the ontogeny of all tetrapods. Small skulls (assumed to be from immature, juvenile individuals) of *Coelophysis bauri* (AMNH 7242, MCZ 4326) have a short rostrum and large orbits relative to overall skull length. One character used in the analysis of Rowe (1989:133) was "antorbital fossa greater than 25% of the length of the skull". The short rostrum on the two small skulls cited above results in an antorbital fossa that is shorter than 25% skull length. If these two specimens were the only two known for *Coelophysis*, and the potential for allometric changes was ignored, the derived state of an antorbital fossa greater than 25% skull length would be confidently coded as absent in the taxon. Luckily, many skulls of larger, more ontogenetically advanced individuals are known for *Coelophysis*, and it is clear that the character is present in the taxon.

At least one author recently chose to eliminate maturity-dependent characters from consideration in phylogenetic analysis (Rauhut, 2003). Characters that involved osteological fusions were the main targets of selective deletion from the analysis. These included a large number of the characters that were used to diagnose Ceratosauria since the early works of Rowe (1989) and Rowe and Gauthier (1990). It was no surprise then

that the analysis of Rauhut (2003) found no support for the inclusion of Coelophysoidea within Ceratosauria.

Two major questions must now be asked. First, if less-than-adult (meaning sub-adult, juvenile, hatchling, and pre-hatchling) individuals constitute all the known specimens of a coelophysoid taxon, and they are scored as if they were adults, does it affect the hypothesis of phylogeny generated by cladistic analysis? Second, if maturity-dependent characters such as osseous fusions, development of processes, and the expression of secondary sexual characters are eliminated a priori from phylogenetic consideration, does it affect the hypothesis of relationship derived from an analysis? The result of not allowing for the ontogenetic stages represented by the available fossil material in phylogenetic reconstruction has not been directly tested. I address these questions below by running three analyses using the same starting data, but optimized to reflect three different approaches to coding characters so as to address the role of ontogeny in coelophysoid theropods.

The four ontogenetic stages cited by Rowe and Gauthier (1990) are not controversial. Most workers would agree that the stages accurately reflect the potential developmental series present any theropod individual, assuming it lived long enough to reach adulthood. There are potential problems in identifying the cut-offs between the ontogenetic stages. Criteria for diagnosing the adult stage of a coelophysoid ceratosaur were given, but only vague references to size and absence of adult characters were cited for the other three ontogenetic stages (Rowe and Gauthier, 1990). This left the task of

distinguishing between a juvenile and sub-adult, and even between a sub-adult and full adult open to broad interpretation.

There was a greater problem with determining the ontogenetic stages assigned by Rowe and Gauthier (1990). Six osseous fusions were cited as the indicators of whether a ceratosaur had attained adulthood by the time of death (see above). But what if only five of the listed co-ossifications were present? Was the individual something between sub-adult and adult? The implication was that the absence of any one of the fusions relegated the individual to sub-adult status. Arguments could be made though that the presence of half, or a majority of the six fusions listed should earn the specimen the status of adulthood.

The issues and arguments that could potentially be raised by the criteria used by Rowe and Gauthier (1990) are analogous to the problems caused by pre-cladistic methods of taxonomy and systematics. The six ontogenetic characters listed by Rowe and Gauthier (1990) acted to define the adult stage of development much as pre-cladistic means of taxonomy defined taxa based upon the characters they possessed. As phylogenetic taxonomists pointed out, the concept that characters define taxa was flawed. New taxa that possessed some, but not all, of the characters used to define higher taxa were problematic in the traditional Linnean classification system because they did not fit the rigid definitions of previously established taxa. Likewise, individual specimens that preserved some of the ontogenetic features listed by Rowe and Gauthier (1990) produced similar problems in classifying their ontogenetic status. The result of such ambiguity was that arguments could be made as to whether or not certain specimens of coelophysoid

ceratosaurs represented adults or not. This had importance in determining how taxa such as *Dilophosaurus* and *Liliensternus* were coded in cladistic phylogenetic analyses.

A Method for Relative Maturity Estimation

The method by which the ontogenetic stage of a fossil organism is determined should undergo a conceptual and methodological revolution, much as the advent of cladistic techniques and phylogenetic taxonomy changed concepts of systematics and classification. This can be accomplished by borrowing the tools and techniques used in cladistic phylogenetic analyses, and applying them to a quantitative ontogenetic analysis.

The first applications of a computer-driven parsimony-based algorithm for ontogenetic stage estimation were by Brochu (1992, 1996). A stated goal of his work was to provide paleontologists a means of accurately assessing whether specimens of fossil crocodylians were from immature members of known taxa, or adult individuals of new, dwarf taxa. This was achieved by examining postcrania of extant taxa (mostly *Alligator mississippiensis*), and evaluating individual skeletal elements for size-independent ontogeny indicators. Ontogenetic stages were then assigned to each skeletal element (e.g., femur, humerus, ilium, etc.), and from them maturity indices could be derived for individuals, thereby ranking their overall degree of osteologic, ontogenetic development. This also facilitated the mapping of the general sequences of ontogenetic events through the ontogeny of taxa. This by-product of the studies was best illustrated by the more-or-less predictable sequence of neurocentral suture fusions, which was used

as a tool for ontogenetic stage estimation in fossil crown Crocodylia (Brochu, 1992, 1996).

The technique proposed by Brochu (1992, 1996) was expanded and elaborated by Colbert (1999), who used a computer-based parsimony algorithm program to score ontogenetic characters in individuals of extant taxa at different stages of maturity, and labeled the technique 'Ontogenetic Sequence Analysis', or OSA (Colbert, 1999). I do not apply the same name to my analysis because it does not utilize all the techniques Colbert (1999) used as integral parts of his OSA. The largest example of his technique was applied to evaluating patterns of craniodental ontogeny in the skulls of the four extant species of the mammal *Tapirus*. The emphasis of the work was directed toward developing a means of recognizing and accounting for polymorphism within a taxon, and demonstrating a means of mapping the numerous and complex pathways available during development. It was also intended to provide a means of making between-species comparisons of developmental pathways, with the hope of uncovering phylogenetically informative data.

An ontogenetic analysis with a similar purpose to that of Brochu (1992, 1996) was recently conducted by Carr and Williamson (2004) to determine the diversity of Maastrichtian tyrannosaurids of North America. Some small tyrannosaurid specimens from these sediments were the basis for erecting new taxa of small tyrannosaurs (Gilmore, 1946; Bakker et al., 1988), whereas others (Carr, 1999; Carr and Williamson, 2004) argued the same specimens were merely immature individuals of the much larger, contemporaneous taxon *Tyrannosaurus rex*. Carr and Williamson (2004) applied a

quantitative ontogenetic analysis approach to the skulls of five individual tyrannosaurids, including specimens that were holotypes for some diminutive tyrannosaurid taxa. Their analysis demonstrated an ontogenetic continuum of cranial features could be plotted between the smallest and largest specimens in their sample, offering support that the small tyrannosaurids from the Maastricthian beds of North America were immature individuals of *Tyrannosaurus rex*, and not pygmy tyrannosaurid taxa (Carr and Williamson, 2004).

Cladistic phylogeny reconstruction does little more than use mathematical, parsimony algorithms to establish a hierarchical arrangement of taxa based upon the distribution of shared derived characters in each taxon. Several computer software applications exist that are designed to quickly perform the algorithmic functions used to generate hypotheses of phylogenetic relationship, and I use the program PAUP* (Phylogenetic Analysis Using Parsimony; Swofford, 2002) here. Programs such as PAUP* require the construction of a taxon-character matrix in which the presence or absence of derived characters (be they morphological structures or nucleotide base pairs) are coded for each taxon in the analysis. The resulting data matrix is then analyzed using the preferred program, and a hypothesis or hypotheses of phylogenetic relationship are generated. The hypothesis of phylogeny is usually then depicted graphically as a branching, hierarchical diagram termed a cladogram. The cladogram illustrates the relative sequence of evolutionary divergences along a lineage, from basal taxa that possess few derived characters, to derived taxa with the greatest number of derived character states (Fig. 3A).

The same programs and techniques can place individual specimens of a single taxon, or closely related taxa into a hierarchical arrangement of relative ontogenetic development (Brochu, 1992, 1996; Colbert, 1999; Carr and Williamson, 2004). Programs such as PAUP* do not differentiate between data entered into it as phylogenetic or ontogenetic in nature. The ontogenetic estimate method differs from cladistic phylogenetic reconstruction in the following ways. First, individual organisms (instead of taxa) are the operational units assessed (Fig. 3B). Second, a specimen-character matrix is constructed to score characters for individual specimens instead of a taxon-character matrix. Third, the graphic depiction of the resulting hierarchical arrangement of specimens is not a cladogram, but is instead an 'ontogram' (Brochu, 1992). The ontogram shows the degree of ontogenetic development (maturity) expressed by individual specimens relative to one another (Fig. 3B).

Characters selected for use in an ontogenetic analysis must have some basis or support for being considered ontogenetic in nature (and ideally they should be easy to identify). A reasonable starting point for identifying some of the patterns of ontogenetic transformations is the examination of growth series of extant taxa. Extant crocodiles and avians present the most appropriate approximations of growth patterns in extinct theropods, given application of an Extant Phylogenetic Bracket approach (Witmer, 1992, 1995, 1997). The work of Brochu (1992, 1996) is a useful guide for recognizing ontogenetic patterns in the postcrania of some Crocodylia. Development in avian embryos (mostly *Gallus*) is well documented, although there is less information

published on post-hatchling changes in the skeleton of avians (Lillie, 1919; Hamburger and Hamilton, 1951; Patten, 1952; Romanoff, 1960; Bellairs and Osmond, 1998).

A large percentage of the ontogenetic characters used by Brochu (1992) were the presence or absence of scars for muscular or ligamentous attachments on the surface of bones. He correctly pointed out that such fine details were often not discernable on fossils and more obvious transformations such as fusions and major shape changes would be more useful. Some examples of uncontroversial ontogenetic characters present in most dinosaurs are co-ossification and fusion between braincase elements, neural arches and vertebral centra, fusion between the atlantal intercentrum and axial centrum, and co-ossification of the exoccipitals and basioccipital within the occipital condyle. More clade-specific ontogenetic characters can and should also be used in the analysis. Fusion between the pelvic bones, co-ossification of the proximal tarsal bones, and fusion between the proximal ends of metatarsals II and III are just some examples of developmental events that occurred at different times along the ontogenetic trajectories of different coelophysoid theropod lineages.

Care must be taken when dealing with characters whose variability may be the result of phylogenetic differences instead of degree of maturity. For example, the nasal bones of *Ceratosaurus nasicornis* were separate early in ontogeny, but in more mature individuals the right and left sides of the nasal horn unique to this taxon co-ossified and fused (Gilmore, 1920; Britt et al., 1999). Within the taxon *Ceratosaurus*, partial fusion of the nasal bones is strictly an indicator of relative maturity. However, fusion between the anterior ends of the nasals was also present in *Rugops primus* (Sereno et al., 2004),

and fusion along the length of the nasals was present in more derived abelisaurids (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Sampson et al., 1998). Therefore, nasal co-ossification may also be an anatomical feature with phylogenetic importance. In this case, listing a character in a phylogenetic analysis does not invalidate its usefulness in an ontogenetic analysis, and visa versa. Many of the phylogenetic features unique to coelophysoid theropods appear only in individuals that reached more mature stages of ontogenetic development. Characters can therefore be present in both ontogenetic and phylogenetic analyses.

There is uncertainty as to the effect of using ontogenetic characters tied to phylogenetic features that are present in some but not all taxa used in the ontogenetic analysis. The character cited above, "fusion between proximal ends of metatarsals II and III" is an example of a feature that's distribution is restricted by both ontogeny and phylogeny. Unfortunately, there is no evidence that the feature was present in the known specimens of basal coelophysoid taxa such as *Dilophosaurus* and *Liliensternus*, whereas it is present in advanced sub-adults and adults of more derived coelophysoids (e.g., *Coelophysis*, *"Syntarsus" kayentakatae*, *Syntarsus rhodesiensis*). This may represent a potential shortcoming of the ontogenetic stage estimation method I promote here in which individuals of multiple taxa are assessed relative to one another. It should not be an issue if the same technique is used to assess multiple individuals of a single taxon.

The character descriptions are written in the format described in detail below (see Chapter 2). There are substantial differences between the format of ontogenetic and phylogenetic character decscriptions and treatments. All ontogenetic characters were

treated as having ordered character states. Unlike phylogenetic characters in which there is a remote chance of skipping intermediate stages of morphological transformations via substantial mutations, ontogenetic development occurs in a fixed direction that requires intermediate steps of transformation (see also Brochu, 1992; Colbert, 1999). An organism cannot reverse its ontogeny. However, the use of ordered reversible characters allowed for reversals to seemingly less mature states. Reversals on the resulting ontograms were interpreted as the expression of individual variation and incompleteness in the sample.

There are a huge number of ontogenetic characters potentially available for use in an ontogenetic analysis. Hypothetically, each and every developmental event that occurs through the ontogeny of each specimen is a character. The pool of characters was restricted to ontogenetic transformations of the skeleton, because the osseous remains are usually the only body components available to paleontologists, and my goal is the interpretation of ontogeny in fossil taxa. I also use only those characters applicable to post-hatchling individuals because there were no verified pre-hatchling specimens of any coelophysoid, or any other purported ceratosaur, known at this time. Most of the characters are based upon the degree of co-ossification between skeletal elements. A few characters are less discrete, and instead take into account less well-defined and recognized indicators of maturity, such as degree of finishing of articular surfaces and bone texture (striated versus smooth). The latter was used as a main indictor of relative maturity by Sampson et al., (1997), and as an ancillary indicator of maturity by Carr (1999).

Some of the characters used in the ontogenetic analysis were not broken down into as many discrete characters as possible. For example, 'sacral neural arches and spines fusion to adjacent arches and spines' was treated as a single discrete character in my analysis. It was at least possible to pull out four separate, discrete characters from the single character given above. They were: (1) fusion between the neural spines of dorsosacral 2 and dorsosacral 1; (2) fusion between the neural spines of dorsosacral 1 and sacral 1; (3) fusion between the neural spines of sacral 1 and sacral 2; (4) fusion between the neural spines of sacral 2 and caudosacral 1. There were not enough coelophysoid specimens with complete and intact sacral neural spines available to be informative for each of these potential characters. They were lumped together into a single discrete character. Ideally, as more coelophysoid specimens are examined and coded for their ontogenetic indicators, these four characters will be treated independently.

The same problems apply to the use of vertebral neural arch and centrum co-ossification characters. The degree of neural arch-centrum co-ossification present in each vertebra should be treated as a separate discrete character. There are few coelophysoid specimens that preserve the entire vertebral series, and even fewer are preserved or prepared adequately to confidently determine the degree of co-ossification between the vertebral components. Some specimens preserve a number of scattered, disarticulated vertebrae. This hinders confident identification of their correct position in the axial series. There is also little overlap in the segments of articulated vertebrae preserved for coelophysoid taxa. For example, the type of *"Syntarsus" kayentakatae* (MNA V2623) preserves a complete, articulated cervical series, but almost none of the dorsal, sacral, or

caudal vertebrae (Rowe, 1989; Tykoski, 1998). The type of *Dilophosaurus wetherilli* (UCMP 37302) preserves a few incomplete cervical centra, but many dorsal and sacral vertebrae. This makes scoring the individual vertebrae and comparing between the two specimens uninformative at this time. Eventually I hope to examine enough coelophysoid specimens to score the neurocentrum suture status of vertebra as a separate discrete character in an ontogenetic analysis.

My ontogenetic analysis differs from the pioneering works of Brochu (1992, 1996) and Colbert (1999) in several significant ways. First, all the taxa in this study are extinct, and there are few known specimens of each taxon. For example, only four partial skeletons (UCMP 37302, UCMP 37303, UCMP 77270, TMM 43646) and a handful of fragments are known of *Dilophosaurus wetherilli*. Only two relatively complete skeletons and a few isolated pieces of *"Syntarsus" kayentakatae* (MNA V2623, TMM 43688-1) are known, and a single incomplete skeleton represents the total sample of *Segisaurus halli* (UCMP 32101) material. The only coelophysoid taxon that might be known from enough specimens to perform a single-taxon analysis is *Coelophysis bauri*. The actual number of *Coelophysis* individuals collected from the Ghost Ranch locality of New Mexico is not known, but estimates range from a few dozen to a few hundred. I did not examine a large number of *Coelophysis* specimens prior to this study. A single-taxon ontogenetic analysis of *Coelophysis bauri* is a future priority that should serve to test the validity of this approach.

The ontogenetic analysis tested individuals from multiple coelophysoid taxa known from adequate material. Assumptions made and potential sources of error

accepted in order to proceed with the ontogenetic analysis. First, I assumed all coelophysoid taxa shared a generally similar pattern of development, regardless of the size difference between some coelophysoid taxa (e.g., *Dilophosaurus* versus *Segisaurus*). Closely related taxa are more likely to have similar patterns of ontogenetic development. The more closely related the taxa, the more alike their ontogenetic development is likely to be. Coelophysoidea is a relatively small clade of theropods, and members of the clade exhibit a high degree of morphological similarity. This is one of the frustrating aspects of studying the clade, for there are often few characters that can readily diagnose and differentiate one coelophysoid from another. The high degree of morphological conservatism and similarity within the clade may indicate that the taxa also retained comparable patterns of growth and development.

Second, I accepted the possibility that individual variation may obscure the ontogenetic signal. The influence of individual variation and polymorphism within a population was highlighted by Colbert (1999). As explained before, none of the coelophysoid taxa used in my ontogenetic analysis were known from enough individuals to conduct a single-species evaluation of polymorphism. There was no way to rule out the possibility that an individual used in the ontogenetic analysis preserved an abnormal or very rarely expressed morphology. A single aberrant individual in the small sample used could have a substantial impact upon the analysis, resulting in an inaccurate placement of an individual on the ontogenetic series and a less-than-optimal reconstruction of coelophysoid developmental transformations.

Third, I accepted that I might mistakenly incorporate a character into the ontogenetic analysis that might later prove to be absent in some taxa. Return again to the example of the fusion between the proximal ends of the second and third metatarsals in *Coelophysis*, *"Syntarsus" kayentakatae*, and *Syntarsus rhodesiensis*. This feature was incorporated into both the ontogenetic and phylogenetic analyses and evaluated for all the taxa in each. No specimen of *Dilophosaurus* and *Liliensternus* exhibits co-ossification between these pedal elements, and the character is coded as missing data in the phylogenetic analysis for both taxa because of the results of my ontogenetic test. The absence of metatarsal co-ossification was attributed solely to the ontogenetic status of the known specimens of both taxa. This assumption was based in part upon negative evidence. It may eventually prove to be that co-ossification between these elements evolved only in *Coelophysis*, *"Syntarsus" kayentakatae* and *Syntarsus rhodesiensis*, and use of the character in the ontogenetic analysis was not warranted.

The selection of specimens included in the ontogenetic analysis of fossil taxa was also more difficult than when dealing with extant taxa. As described above, there are few coelophysoid specimens that are complete skeletons. The holotype of *Syntarsus rhodesiensis* (QG1) and the published specimens of *Liliensternus liliensterni* (treated as two individuals by Huene [1934], but they may possibly representing more than two) were scored from the literature (Huene, 1934; Raath, 1969, 1977, 1990). I did not include any specimens of *Coelophysis* in the analysis, even though the taxon will probably provide the best data concerning growth and development in a coelophysoid theropod. The current state of knowledge concerning the details of anatomy in the taxon

is not yet adequate for an analysis of this type. There are serious inconsistencies between descriptions and illustrations of important anatomical features and the reality present in fossil material. *Coelophysis* specimens will be added to future analyses after more thorough, first-hand examination. Specimens of *Dilophosaurus wetherilli* and *"Syntarsus" kayentakatae* were examined first-hand.

My analysis also differed from those of Brochu (1992, 1996) and Colbert (1999) in its anatomical scope. Brochu (1992, 1996) concentrated upon a number of postcranial elements only. Colbert (1999) applied his technique to published data of human hand and wrist development, as well as observations of craniodental development in *Tapirus*. The ontogenetic analysis recently conducted by Carr and Williamson (2004) concentrated only on ontogenetic transformations in the skull of tyrannosaurids. I included data from all parts the skeleton, wherever enough overlap in preserved elements was present between the few coelophysoid specimens available. Ideally, every element of a skeleton will yield characters that can help establish relative ontogenetic stages of coelophysoid specimens.

The final substantial difference between my ontogenetic analysis and those of Brochu (1992, 1996) and Colbert (1999) was the ultimate purpose behind each study. The patterns of osteological development in extant taxa were derived by Brochu (1992, 1996) to assess the adult status of fossil crocodylomorphs. The focus of Colbert (1999) was to establish a means of reconstructing the developmental pathways available to taxa given the vast amount of polymorphism in a natural population. As he stated, his technique, "is applicable to any of the multitude of developmental sequences occurring

during the entire span of ontogeny in any taxon" (Colbert, 1999: 57). The technique was not applied to any extinct or fossil taxa at that time.

The primary goal of the ontogenetic analysis was to use a modified version of the technique pioneered by Brochu (1992, 1996) to determine the relative degree of ontogenetic development of coelophysoid theropod fossils and apply that knowledge directly to character coding in a cladistic analysis of basal theropod phylogeny. To reach this goal, I first had to generate a reproducible, testable, set of ontogenetic characters diagnostic of the development of coelophysoid theropods. In other words, the developmental events that occurred during growth in coelophysoids needed to be identified and mapped. The establishment of such a list of diagnostic ontogenetic characters will provide an aide for future workers who seek to accurately assess the ontogenetic status of new specimens. This should then prevent some of the problems encountered during previous phylogenetic studies of the group, and ultimately result in more accurate reconstructions of basal theropod evolution.

Ontogenetic Analysis: Methods and Materials

The ontogenetic analysis was run using PAUP* Version 4.0b10 for Macintosh (Swofford, 2002). The specimen-character matrix was created using MacClade 4.03 (Maddison and Maddison, 2001). Both were run on an Apple Macintosh G4 computer (400Mhz processor) with a minimum of 100MB of RAM allocated to PAUP* during its operations. Specimens representing 14 individuals from six coelophysoid taxa were included as members of the ingroup. They are listed in Table 2. Rooting was based on

the outgroup method, and PAUP* was set to make the ingroup monophyletic and the outgroup paraphyletic with respect to the ingroup. A single hypothetical outgroup individual with all character states scored as absent was used to polarize the character states. Use of a single hypothetical outgroup should be avoided in phylogenetic analyses because of the a priori assumptions of character polarity implied by such an act. In contrast, ontogenetic development has a predictable starting point (fertilization) that lacks ossified tissues, so I accepted the use of a zero-state hypothetical outgroup.

Forty-seven parsimony-informative characters were coded in the data matrix. The characters are listed in Appendix 2. The character-specimen matrix is given in Appendix 3. Multistate characters were allowed, and all characters were treated as ordered characters to reflect the unidirectional nature of ontogenetic development, while still allowing the possibility of individual variation (expressed as reversal). Characters scored with multiple states in the same specimen (0/1, or 0&1) were interpreted to be the result of uncertainty rather than polymorphism because of the often incomplete condition of the specimens. Searches were conducted using a heuristic (branch swapping) search algorithm. The branch swapping algorithm used tree-bisection reconnection (TBR). Starting trees were obtained by stepwise addition, with a simple addition sequence. The distribution of character state transformations on the resulting hypotheses of ontogenetic development was mapped using both ACCTRAN (accelerated transformations) and DELTRAN (delayed transformation) character state optimizations.

Most of the multistate characters in the analysis encompass the degree of sutural co-ossification between two osseous elements. The possible character states in most

cases are open (= co-ossification absent, elements might not even have tight contact), suture present but clearly visible (= co-ossification minor, may be interdigitation between elements), and fusion present, suture closed or obliterated (= co-ossification complete, separate elements virtually indiscernable). Examples of these potential character states are shown in Figure 4.

Ontogenetic Analysis: Results

The ontogenetic analysis resulted in 3645 equally most parsimonious hypotheses of relative ontogenetic development, each with a length of 81, a consistency index (C.I.) of 0.9259, and a retention index (R.I.) of 0.9531. The high number of equally most parsimonious hypotheses is probably a result of the large amount of missing data for most of the specimens. Strict, 50% majority rule, and Adams consensus ontograms of the resulting hypotheses are shown in Figure 5. Specimens of *Dilophosaurus* (UCMP 77270), *"Syntarsus" kayentakatae* (MNA V2623), *Syntarsus rhodesiensis* (QG 1), and the Shake-N-Bake taxon (MCZ 9442, MCZ 9463, TMM 43689-4) clustered in a polytomy as the most mature individuals in the analysis on the strict consensus ontogram (Fig. 5A). I chose the node shared by these specimens on the strict consensus ontogram as the minimum boundary of the adult stage of coelophysoid ontogenetic development.

I would prefer to avoid setting up boundaries for juvenile and sub-adult stages because these represent arbitrary designations on a broad continuum of ontogenetic development. There is some utility in having a general designation of maturity level when communicating the status of individual specimens. So, for the sake of easy communication I denoted boundaries for these less-than-adult stages. There are no clear-

cut nodes on the strict consensus that adequately delineate the boundaries for juvenile and sub-adult stages of maturity. Two specimens (UCMP 32101 *Segisaurus*; TMM 43688-1, *"Syntarsus" kayentakatae*) were placed just outside the adult stage node, and were considered sub-adults. All the remaining specimens cluster in a basal polytomy in the strict consensus ontogram.

The 50% majority rule and Adams consensus ontograms provided better indications for establishing the boundaries of the juvenile and sub-adult stages. The sub-adult stage of Rowe and Gauthier (1990) was defined as including individuals of near maximum size but lacking signs of growth cessation. This is difficult to establish in taxa for which no adult specimen is known (e.g., *Liliensternus*, *Segisaurus*). The ontogenetic analysis did include one taxon represented by multiple individuals of variable sizes, including one unambiguous adult. *"Syntarsus" kayentakatae* was represented by three specimens in the analysis (MNA V2623, TMM 43669-3, TMM 43688-1). As mentioned above, MNA V2623 fell solidly within the adult stage on the strict consensus ontogram, and TMM 43688-1 was consistently just outside the boundary of the adult stage (Fig. 5A). I assumed that the latter specimen was near the upper end of the sub-adult maturity stage. The third individual (TMM 43669-3) fluctuated in position between the 50% majority rule and Adams consensus ontograms (Figs. 5B, C). The individual was approximately 70% the size of MNA V2623 at the time of death, as measured across the mediolateral width of the proximal tarsals. It also lacked most of the co-ossifications used as size-independent maturity indicators in the ontogenetic analysis (see below). I

therefore considered this individual a juvenile, albeit a relatively mature juvenile given its position in the majority rule and Adams consensus ontograms (Figs. 5B, C).

Dilophosaurus was represented by only a single adult individual (UCMP 77270) (Fig. 5A). The three remaining specimens of the taxon (TMM 43646, UCMP 37302, UCMP 37303) are all remains of relatively immature individuals. These include the type (UCMP 37302) and referred (UCMP 37303) specimens described by Welles (1984). These results are generally consistent with the size difference between what is probably the least mature *Dilophosaurus* specimen (TMM 43646) and the most mature (UCMP 77270). The femur of TMM 43646 is approximately 75% the length of the femur in UCMP 77270. The Adams consensus of the resulting ontograms (Fig. 5C) also indicated that the single adult of *Dilophosaurus* (UCMP 77270) was less mature than adults of *"Syntarsus" kayentakatae*, *Syntarsus rhodesiensis*, and the Shake-N-Bake taxon in the analysis. The tarsals and pes of UCMP 77270 are not preserved, areas that possess several of the ontogenetic characters used in my analysis. The fact that these characters had to be scored as missing data may have influenced the outcome of the analysis, pulling UCMP 77270 to a less mature position in the ontogenetic hypotheses.

Liliensternus was represented by two relatively immature individuals (catalogued together under MB R 2175) in the ontogenetic analysis. The specimens were originally divided out as large and small individuals by Huene (1934), but as was pointed out (Rauhut, 2003), the material is difficult to clearly separate, and may even represent more than two individuals. I retained the use of large and small individuals in the analysis. Both individuals clustered in a basal polytomy of immature individuals in the strict

consensus ontogram (Fig. 5A). The Adams consensus provided better resolution, with the smaller individual one of the more ontogenetically developed of the least mature individuals, and the larger individual fell out near the middle of the ontogenetic series of specimens (Fig. 5C). Both of these specimens were incomplete, and were scored from the literature and some photographs.

Segisaurus was represented in the analysis by only a single specimen, the type (UCMP 32101). It was solidly positioned within the sub-adult stage of all the consensus ontograms (Fig. 5). This has implications for the validity of the Shake-N-Bake taxon, which is known from at least one fully adult specimen (MCZ 9442; incomplete pelves and synsacrum) that is smaller than the corresponding elements preserved in the partial skeleton of *Segisaurus*.

Syntarsus rhodesiensis was also represented by only a single individual (QG 1) in my ontogenetic analysis, even though numerous specimens are known of the taxon (Raath, 1977, 1990). I scored this taxon from the available literature. The type (QG 1) was the only specimen of the taxon that was well described and figured, and also possessed a large number of elements unambiguously referable to a single individual. The specimen was solidly nested among the adults in the ontogenetic analysis (Fig. 5).

The three specimens of the Shake-N-Bake taxon (MCZ 9442, MCZ 9463, TMM 43689-4) are all from adult individuals, if the hypotheses of relative ontogenetic maturity retrieved here is valid (Fig. 5A). This was somewhat surprising given the small size of the elements tested, as well as the large amount of missing data coded for each of the three fragmentary specimens. This lends further support to the claim that the remains

from the Shake-N-Bake locality represent a new, diminutive coelophysoid taxon (Tykoski, 1997, 1998).

The primary purpose for conducting the ontogenetic analysis was to determine the relative ontogenetic stage of coelophysoid specimens, with the goal of identifying individuals of comparable maturity for use in correctly scoring characters among the representative taxa. The results were incorporated into my phylogenetic analysis in Chapter 2. A secondary outcome of the analysis was the ability to map the generalized pattern of ontognetic transformations that occurred through the life history of a coelophysoid theropod. Figure 6 is one of the 3645 equally most parsimonious ontograms generated by the analysis. This particular ontogram was selected for illustrative purposes because the arrangement of specimens in the hypothesis of ontogeny was generally similar to the topography of the 50% majority rule and Adams consensus ontograms. The boundaries of the juvenile, sub-adult, and adult stages of maturity are given on the ontogram. The distribution of ontogenetic transformations was traced using both ACCTRAN and DELTRAN character state optimization criteria. The unambiguous ontogenetic characters that diagnose each node up to the adult stage minimum boundary are mapped in Figure 6. Table 3 is a tabulation of the sequence of ontogenetic transformations hypothesized to have occurred in coelophysoid theropods at each of the nodes (labeled with Roman numerals) on Figure 6.

Several ontogenetic transformations (both unambiguous and ambiguous) diagnosed the adult stage on the ontogram, facilitating easy recognition of adult specimens during examination. The largest specimen of *Dilophosaurus* (UCMP 77270)

is the least mature adult on the ontogram. The ontogenetic transformations exhibited by specimens more mature than UCMP 77270 also are useful indicators of adulthood in coelophysoid taxa, and care should be taken to look for them when attempting to assess the ontogenetic stage of a given specimen. To reiterate, the potential character states in most cases were open (= co-ossification absent, elements might not even have tight contact), suture present but clearly visible (= co-ossification minor, may be interdigitation between elements), and fusion present, suture closed or obliterated (= co-ossification complete, separate elements virtually indiscernable) (Fig. 4).

Discussion

Most of the ambiguity concerning the presence or absence of certain characters in adult coelophysoids in the analysis was a result of missing data. For example, all of the ambiguous characters that diagnosed a minimal adult coelophysoid under ACCTRAN optimization were missing in UCMP 77270. All of the potentially diagnostic but ambiguous pelvic and sacral characters listed under DELTRAN optimization for the same node were missing in MNA V2623. This was the result of the incomplete condition of most coelophysoid fossils. It also served to further illustrate the need to include specimens from multiple taxa in order to achieve any level of resolution in ontogenetic stage reconstruction.

The ontogenetic analysis clearly showed that three of the four relatively complete specimens of *Dilophosaurus wetherilli* are the remains of immature individuals. UCMP 37303 is an incomplete specimen that preserves few of the elements from which the

ontogenetic characters in this analysis were derived. The degree of character incompleteness (only 8.5% of characters present) of the specimen might have pulled it relatively lower on the ontogram, as is apt to occur with incomplete specimens in a phylogenetic analysis. TMM 43646 is a more complete and well-preserved specimen of *Dilophosaurus* that is still undergoing preparation and study. It is a slightly smaller individual than UCMP 37302 and 37303, but lacks almost all the developmental transformations present in the other coelophysoid specimens. UCMP 77270 is the only known specimen of *Dilophosaurus wetherilli* that represents the remains of an adult individual. This specimen was not included in the monographic description of the taxon by Welles (1984) because he hypothesized that it represented a taxon distinct from the type and referred specimens (UCMP 37302, UCMP 37303). As a result, misconceptions and errors concerning parts of the anatomy of *Dilophosaurus* were perpetuated for years. These had profound effects upon phylogenetic reconstructions of ceratosaur and basal theropod phylogeny (see below).

Liliensternus liliensterni also is represented only by the remains of immature individuals. *Liliensternus* is one of the largest theropods known from Late Triassic age sediments, yet it is likely that even the larger individual is not an adult. Previous phylogenetic analyses (Carrano et al., 2002; Rauhut, 2003) coded *Liliensternus* as if the specimens were adults. My ontogenetic analysis suggests such treatment was in error. For example, the characters, 'cervical ribs and centra fused in adults', and 'fusion of pelvic elements in adults', were scored as unambiguously absent in *Liliensternus* by Carrano et al. (2002). Yet my ontogenetic analysis indicates that there are no adult individuals of

Liliensternus known. This means that these character states could not be evaluated in the taxon. The absence of the above-mentioned features in the skeleton of the known *Liliensternus* individuals was probably the result of immaturity, and not phylogeny. Such late-appearing, maturity-dependent characters must be re-assessed for the taxon, and should be scored as missing data.

The type and only known specimen of *Segisaurus halli* (UCMP 32101) falls in the middle of the relative ontogenetic sequence of coelophysoids, and is considered a sub-adult. It shares a number of ontogenetic transformations with the adult specimens in the analysis. These include a pronounced trochanteric shelf at the base of the anterior trochanter, and an oblique ridge on the medial surface of the proximal fibula. The scapula and coracoid are sutured, but a clearly visible line of contact remains between them. The skeleton also lacks the complete closure of pelvic sutures. The specimen is missing almost all of the dorsal vertebral series, as well as most of the sacrum and the dorsal parts of the ilia. As a result, many ontogenetic characters could not be assessed for the specimen and were left as missing data.

The same features are also present on TMM 43688-1, a specimen of *"Syntarsus" kayentakatae* that is much larger than the holotype of *Segisaurus halli*. TMM 43688-1 is currently represented by mostly sacral, pelvic, and hindlimb elements. Much more of the skeleton of TMM 43688-1 remains jacketed and unprepared, including many more vertebrae, at least part of the pectoral girdle, and forelimb bones. The quality of preservation of this specimen is excellent, so preparation of the remaining pieces should uncover considerable data for both ontogenetic and phylogenetic consideration. The

specimen is a sub-adult of nearly adult size as compared to the holotype (MNA V2623). It was excluded from the adult stage in the ontogenetic hypotheses by the lack of suture or fusion between the sacral ribs and ilia.

The holotype of *"Syntarsus" kayentakatae* (MNA V2623) is an adult individual that exhibits the fully mature adult condition of all the ontogenetic characters observable in the specimen. Cranial elements are thoroughly bound. Some sutures, such as between the quadrate and quadratojugal, are nearly indiscernible. The scapulocoracoids are solidly fused, as are the tibiotarsi and tarsometatarsi. The specimen is missing almost all of the post-cervical vertebral column, as well as most of the pelves. The missing data from these parts of the skeleton was probably the only reason the specimen did not fall out as the most ontogenetically mature coelophysoid individual in the analysis.

The three specimens from the Shake-N-Bake taxon are of special interest. MCZ 9442 is a three-dimensionally preserved partial synsacrum, missing the last sacral vertebra (caudosacral 1), anterior and posterior parts of the ilia, distal parts of the pubes, and distal ischia. It was scored for 44.7% of the characters in the ontogenetic analysis. The other two Shake-N-Bake specimens are among the least complete specimens in the study. MCZ 9463 is a distal tibiotarsus that preserves only 6.4% of the available characters. TMM 43689-4 is a proximal tarsometatarus that preserves the proximal parts of the fused metatarsals II and III with distal tarsal III fused to its metatarsal, the proximal end of metatarsal IV, and distal tarsal IV. It preserves only 4.3% of the characters in the analysis. All three specimens were placed among the adult coelophysoid specimens in the analysis. MCZ 9463 is a fully fused distal tibiotarsus,

with the astragalus and calcaneum also fused to form an astragalocalcaneum. The mediolateral width of the proximal tarsals of the specimen is slightly more than half as large as in a juvenile specimen of *"Syntarsus" kayentakatae*, TMM 43669-3. This supports earlier claims (Tykoski, 1997, 1998) that the Shake-N-Bake fossils represented the remains of a new diminutive coelophysoid taxon. They are not juvenile remains of either *"Syntarsus" kayentakatae* or *Dilophosaurus wetherilli*, for which far larger but less mature individuals are known.

The information retrieved from the ontogenetic analysis can now be applied to a phylogenetic analysis of basal theropod relationships. The ontogenetic analysis (Figs. 5A, 6) showed that the taxon *Liliensternus liliensterni* is not represented by any adult remains. Therefore, maturity-dependent characters that are expressed only in advanced sub-adults (such as TMM 43688-1) and adults cannot be assessed for *Liliensternus*. Such characters should be scored as missing data in a phylogenetic analysis. Remains of at least one adult *Dilophosaurus wetherilli* are known (UCMP 77270), and many maturity-dependent characters can be evaluated and scored from it. There remain some characters, such as those pertaining to the metatarsus, that should not be scored for *Dilophosaurus* because the only adult specimen (UCMP 77270) does not preserve the elements in question. Character coding for all the other coelophysoid taxa in my phylogenetic analysis should also reflect the ontogenetic status of the referenced and examined fossil material.

CHAPTER 2

Phylogenetic Analysis: Methods and Character Descriptions

The first application of cladistic methodology to phylogeny reconstruction within Saurischia was by Gauthier (1986). The ever-increasing processor speed and memory capacity of computers coupled with improvements in the ease of use of the available software allowed analyses to increase in size with regards to both the number of taxa and the number of characters that could be scored for the taxa. Some of the more notable works that influenced current understanding of theropod relationships include those of Holtz (1994, 1998), Sereno et al., (1994, 1996), Sereno (1999a), Carrano et al. (2002), and Rauhut (2003).

The authors cited above are not consistent in their results, particularly with regard to the composition of Ceratosauria and the relationships of taxa that diverged near the base of Theropoda. A number of variables can alter the results achieved by different workers, even when the same specimens are examined and scored for a given character set. The more important of these potential variables are discussed here.

The greatest influence upon the results obtained in these studies is probably access to the material. Most Mesozoic theropods are known from incomplete specimens, and many are represented by a single specimen. This places a high premium upon the value of these specimens in their respective institutions and repositories, which may result in restricted access to outside researchers. Also, specimens important for basal theropod relationships are stored in facilities on at least four continents. It is logistically

difficult for researchers to examine all the pertinent theropod material first-hand. More workers are forced to rely to some degree upon published descriptions of fossil theropods when scoring character-taxon matrices. In doing so, mistakes or misinterpretations made in original descriptions or analyses are perpetuated. I acknowledge that scoring character states using only published descriptions and figures is less than ideal, but I too must rely heavily upon this practice for a large number of the taxa in my analysis.

Different interpretations of anatomy, as well as interpretations of the character state descriptions are a source of discrepancy. Our understanding of potentially homologous structures in the anatomy of fossil taxa change as more taxa are discovered and additional intermediate stages of character development are recognized. Better preparation of material can uncover features previously unknown or poorly exposed in long-known specimens, requiring alteration of character coding in subsequent studies. Cursory examination of specimens can lead a scientist to believe they have a thorough understanding of particular specimens or taxa, yet more detailed scrutiny of the same specimens often provides more information, or even contradicts the conclusions reached during a hurried examination.

I also argue that correct assessment of the ontogenetic stage of the material representing taxa has the potential to affect the outcome of phylogenetic hypotheses. As demonstrated in Chapter 1, some of the taxa pertinent to phylogeny reconstruction of basal Theropoda are known only from immature material. The inclusion of juvenile and sub-adult material in cladistic phylogeny reconstruction might have an adverse effect upon phylogenetic hypotheses if ontogenetic stage at time of death of the representative

specimens is not taken into account. This is especially important when character-taxon matrices contain maturity-dependant characters. Many skeletal characters are not expressed until later in ontogeny. Part of my study tests the impact of different assumptions regarding assessing maturity at the time of death of relevant specimens, using the results obtained from the ontogenetic analysis in Chapter 1.

The primary goal of my work is to retrieve a more robust hypothesis of basal theropod relationships than those put forth by previous workers. I seek to accomplish this by bringing new specimens and characters to bear, and by testing assumptions regarding specimen maturity and character coding. Recent extensive phylogenetic tests produced hypotheses of theropod relationships with Coelophysoidea positioned as the proximal outgroup to a *Dilophosaurus* + Neotheropoda (see Table 1) clade (Carrano et al., 2002; Rauhut, 2003; Fig 1C). My detailed examination of coelophysoid fossils, particularly those collected from the Kayenta Formation of northern Arizona, provides information not available to other authors. Also, my character matrix reflects the results of a quantitative ontogenetic analysis that determines the relative maturity of individual specimens, a practice only informally attempted in earlier studies of basal theropod phylogeny reconstruction (Gauthier, 1986; Rowe and Gauthier, 1990).

Phylogenetic Methods

The cladistic phylogenetic analyses of theropod relationships conducted over the past decade are cumulative in the sense that they are expansions of previous studies that incorporate the character-taxon matrices used by previous authors, add new characters

and taxa, and reinterpret and re-code previous characters and anatomy. My study is similar in this regard, although it also brings new specimens of previously known taxa to bear. Three previous studies formed much of the basis for my work. They were those of Holtz (1998), Carrano et al. (2002), and Rauhut (2003).

The analyses of Holtz (1998) and Rauhut (2003) were extensive and incorporated members of all the major clades of Mesozoic theropods, including highly derived coelurosaurians. I differ from them in that derived coelurosaurian taxa are not included. The addition of such derived taxa is not likely to improve the resolution of basal theropod relationships. Their presence is likely to increase the amount of homoplasy in the study because of convergence of some anatomical features in the sacrum, pelvis, and tarsus of coelophysoids and derived coelurosaurs. These features are not present in many taxa and clades more derived than coelophysoids and less derived than coelurosaurs, so there is little danger that exclusion of the latter represents a loss of potential phylogenetic information.

All analyses were run using PAUP* Version 4.0b10 for Macintosh (Swofford, 2002). The data matrix was created using MacClade 4.03 (Maddison and Maddison, 2001). Both applications were run on an Apple Macintosh G4 computer (400Mhz processor) with a minimum of 100MB of RAM allocated to PAUP during its operations. The primary taxon-character matrix consisted of 264 parsimony-informative characters, scored for 4 outgroup taxa and 28 ingroup taxa. Rooting was based on the outgroup method, and PAUP was set to make the ingroup monophyletic and the outgroup paraphyletic with respect to the ingroup. The matrix consisted of binary and multi-state

characters. Taxa that exhibited multiple states for a given character were coded as missing data ("?") if the morphological condition was uncertain, and scored as both absent and present ("0&1") if there was evidence for polymorphism. Searches were conducted using a heuristic (branch swapping) search algorithm because of the size of the character-taxon matrix. The branch swapping algorithm used tree-bisection reconnection (TBR). Starting trees were obtained by stepwise addition, with a simple addition sequence. The distribution of character state transformations on the resulting hypotheses of phylogeny was mapped using both ACCTRAN (accelerated transformations) and DELTRAN (delayed transformations) character state optimizations.

Compound clades were not used as operational taxonomic units (OTU). The lumping of several taxa into a single OTU is common in large analyses, especially for outgroups and clades that are widely accepted and not controversial with regard to their monophyly (Holtz, 1998; Sereno, 1999; Rauhut, 2003; Sereno et al., 2004). For example, Ornithischia was an outgroup OTU in several studies (Holtz, 1998; Sereno, 1999; Rauhut, 2003). The works did not state whether Ornithischia was coded based upon features found in a single taxon, in multiple taxa, in basal members of the clade, or more derived taxa. Only individual taxa are coded in this analysis. Table 4 provides a list of all the taxa used as OTUs in this study, including the full binomial for each taxon. Use of a single nomen elsewhere in this work (e.g., *Dilophosaurus*) refers to the specific taxon listed in Table 4 (e.g., *Dilophosaurus wetherilli*). The published works from which each taxon was scored and lists of specimens that were personally examined for the analysis

are also given in Table 4. Table 5 lists all the OTUs considered in this study and the relative degree of completeness for each OTU in the taxon-character matrix.

Outgroup selection

Most of the previous large analyses of basal theropod relationships lacked adequate taxonomic sampling in outgroup selection. For example, a "compromise outgroup" was erected by Holtz (1998:9) to establish character polarity. *Eoraptor lunensis*, herrerasaurids, and basal sauropodomorphs were collectively considered 'primitive' taxa relative to the ingroup. Characters present in some of these three taxa, but not all, and also present within the ingroup were scored as 'derived', as well as all those characters missing entirely from the three outgroup-contributing taxa but present in some or all ingroup taxa. This convoluted outgroup treatment was an attempt to reconcile issues of the placement of *Eoraptor* and the herrerasaurids as either basal saurischians or basal theropods.

A different approach was taken by Carrano et al. (2002), who used only *Eoraptor lunensis* and *Herrerasaurus ischigualastensis* as successively closer outgroup taxa to the rest of Theropoda. This assumed theropod affinities of these two taxa, an assumption questioned by the results of other, independent analyses (Gauthier, 1986; Holtz and Padian, 1995; Langer, 2004). Use of only two outgroup taxa is a potential problem, because in the case where character states are split between the two, character polarity is unclear for ingroup consideration (Maddison et al., 1984). Three outgroup taxa were used by Rauhut (2003), the basal archosaur *Euparkeria capensis*, the ornithodiran

Marasuchus lilloensis, and Ornithischia (a compound OTU). Unlike previous works, *Eoraptor* and *Herrerasaurus* were treated as ingroup taxa for that study, as well as Sauropodomorpha (another compound OTU).

A denser sample of outgroup taxa was sought for use in my primary analyses, so as to reduce problems of ambiguous character polarity resulting from insufficient outgroup selection and hopefully resolve the issue of the phylogenetic positions of *Herrerasaurus* and *Eoraptor*. A number of 'pre-tests' were conducted that used the data matrix described above. The outgroup-selection pre-test analysis initially utilized only four outgroup taxa. They were *Marasuchus lilloensis*, the ornithischians *Lesothosaurus diagnosticus* and *Scutellosaurus lawleri*, and the well-known sauropodomorph *Plateosaurus longiceps*. All other taxa were identified as ingroup taxa (see discussion of ingroup selection below) in PAUP*, including *Herrerasaurus* and *Eoraptor*. The pre-test analyses showed *Herrerasaurus ischigualastensis* was the most basal member of the theropod lineage, the proximal outgroup to *Eoraptor* + Neotheropoda (see Chapter 3; Fig. 108).

Lesothosaurus diagnosticus and *Scutellosaurus lawleri* represented Ornithischia in the analysis. *Lesothosaurus* is the most basal ornithischian for which a large percentage of the skeleton is known. *Scutellosaurus* is usually considered a basal member of the thyreophoran lineage of ornithischians because of an extensive array of osteoderms on the animal's dorsal surface (Colbert, 1981). *Scutellosaurus* is osteologically very similar to *Lesothosaurus*, and between the two taxa most of the elements of the skeleton are represented. *Scutellosaurus* is currently known only from

the same Kayenta Formation deposits that yielded many of the coelophysoid specimens considered in this study. There are numerous specimens referred to *S. lawleri* in the collections of the TMM, and many were examined first-hand during scoring of the taxon (Table 4).

The details of basal sauropodomorph phylogeny are not well understood. Traditionally, 'prosauropods' were viewed as a paraphyletic colletion of taxa successively closer to Sauropoda (Romer, 1956; Gauthier, 1986). A number of large cladistic analyses of sauropod phylogeny are now published (Upchurch 1995, 1998; Wilson and Sereno, 1998; Wilson, 2002). All of these works assumed a monophyletic Prosauropoda as sister taxon to Sauropoda, as per Sereno (1999a). A recent cladistic analysis found Prosauropoda to be a monophyletic clade and the sister taxon to Sauropoda (Galton and Upchurch, 2004). *Plateosaurus* was selected for my study as a representative basal sauropodomorph. The taxon *Plateosaurus* has undergone considerable taxonomic revision, and the abundant, well described specimens from the Trossingen area of Germany were assigned to *Plateosaurus longiceps* (instead of *P. engelhardti*) by Galton and Upchurch (2004). *Plateosaurus* was one of the most derived prosauropods (Sereno, 1999a; Galton and Upchurch, 2004). It is desirable to select basal members of clades for outgroup comparison because they are likely to possess fewer autapomorphic character states that may obscure or modify the ancestral states shared by it and the ingroup taxa. *Plateosaurus* may be derived among prosauropods, but it is one of the few taxa for which virtually the entire skeleton is known and well figured in the literature. The recently

discovered basal sauropodomorph *Saturnalia tupiniquim* (Langer et al., 1999; Langer, 2003) should prove an important outgroup taxon for future analyses.

Ingroup selection

Ingroup taxa were chosen on the basis of several criteria. Those taxa that were at some point in the past included within Ceratosauria were initially selected for inclusion in the study. My analysis differs from most recent cladistic analyses that include coelophysoid theropods in one important respect. Most of the recent studies score *Syntarsus* as a single OTU, or lump *Syntarsus* with *Coelophysis bauri* in the compound OTU Coelophysidae (Holtz, 1998; Carrano et al., 2002; Rauhut, 2003). The sister taxon status of the two *Syntarsus* taxa was established only in some of earliest cladistic analyses of Ceratosauria (Rowe, 1989; Rowe and Gauthier, 1990). The hypothesized sister-taxon relationship of the two forms has not been thoroughly tested since. Both purported *Syntarsus* taxa (*S. rhodesiensis* and *"S." kayentakatae*) are treated as separate OTUs in my analysis. I do not use Coelophysidae as an OTU.

Second, a number of basal tetanuran taxa common to the previous major cladistic analyses of Theropoda were selected. Preference was given to those taxa that are well described and figured in the literature, or for which a high percentage of characters were scored in prior studies. These taxa included *Torvosaurus tanneri*, the spinosaurids *Baryonyx walkeri*, *Suchomimus tenerensis*, and *Irritator challengeri* (treated as a compound OTU by Holtz [1998] and Rauhut [2003], and omitted by Carrano et al., [2002]), *Eustreptospondylus oxoniensis* (referred to the taxon *Magnosaurus oxoniensis*

Huene by Rauhut [2003]), *Allosaurus fragilis*, and *Ornitholestes hermanni*. *Eoraptor lunensis* and *Herrerasaurus ischigualastensis* were also incorporated as part of the ingroup. *Eoraptor* was scored from first-hand examination of the skull of the type specimen (PVSJ 512), as well as from a cast of the type skeleton (TMM 43451-2).

Eustreptospondylus (*Magnosaurus*) *nethercrombiensis* and *Eustreptospondylus* (*Magnosaurus*) *oxoniensis* were not differentiated by Rauhut (2003), but rather were treated as a single OTU. *Eustreptospondylus oxoniensis* was listed by Holtz (1998) as the taxon scored in his analysis, whereas only *Eustreptospndylus* was indicated as an OTU by Carrano et al. (2002) without indication of the particular species. It is likely that *E. oxoniensis* was used in the latter analysis, because the specimen upon which the taxon is based is more complete than *E. nethercrombiensis*, expecially with regard to cranial material.

Three spinosaurid taxa, *Baryonyx walkeri*, *Suchomimus tenerensis*, and *Irritator challengeri* were included in my analysis. It may first appear redundant to use so many spinosaurid taxa. All of these taxa were included because among them most parts of the spinosaurid skeleton were represented in the literature (Charig and Milner, 1997; Sereno et al., 1998; Sues et al., 2002). *Spinosaurus aegyptiacus* was not included with the other spinosaurids because of the incompleteness of the type (now destroyed) specimen (Stromer, 1915).

Several theropod taxa that were previously allied with ceratosaurs or coelophysoids in the past were represented by incomplete and potentially non-diagnostic specimens. Several pre-test analyses were conducted to identify and eliminate taxa that

were used in previous cladistic analyses of basal theropod relationship, but proved highly labile and offered little contribution to resolving resolution among the more complete and stable ingroup taxa. These taxa included *Camposaurus arizonensis*, *Gojirasaurus quayi*, *Procompsognathus triassicus*, *Genusaurus sisteronus*, and *Shuvosaurus inexpectatus*. In most cases, the incorporation of one of these taxa resulted in thousands of additional equally most parsimonious hypotheses of relationship between the ingroup taxa, and greatly reduced resolution within the coelophysoid or ceratosauroid lineage respectively. Inclusion of all of these taxa resulted in more than a quarter-million equally most parsimonious trees, with basal polytomies within Coelophysoidea and Ceratosauroidea in the strict consensus tree. Each of these problematic, labile taxa is briefly discussed here. A brief discussion of the temporal context and phylogenetic positions of these taxa is found in the discussion section of Chapter 3.

The type of *Camposaurus arizonensis* (UCMP 34498) consists of a pair of distal tibiotarsi that show fusion between their respective elements (Long and Murry, 1995; Hunt et al., 1998). This includes fusion between the fibula and calcaneum (also seen in the type of *"Syntarsus" kayentakatae*) and between the tibia and fibula on their posterior surface just proximal to the astragalar contact. When fibula-calcaneum fusion was added to the phylogenetic analysis as a new character, *Camposaurus* consistently came out as the sister taxon to *"Syntarsus" kayentakatae*. When the character was removed from the matrix, and fibula-calcaneum fusion was treated strictly as the result of ontogeny and not phylogeny, *Camposaurus* was very labile and destroyed resolution between those coelophysoids more derived than *Dilophosaurus* and *Liliensternus* in the strict consensus

tree. *Camposaurus* was found to be in a basal polytomy with the Shake-N-Bake taxon, a *Syntarsus rhodesiensis* + *Coelophysis* clade, and a "*Syntarsus*" *kayentakatae* + *Segisaurus* clade in both the majority rule and Adams consensus trees. *Camposaurus* also lacked any unique apomorphies distinguishing it from other coelophysoids. Its status as a valid, diagnosable taxon is therefore in doubt.

Several isolated skeletal elements from the same locality as the type tibiotarsi could be from the same individual. These include a proximal femur (UCMP 139662), a partial synsacrum (UCMP 138591), and a piece of the right pelvic girdle that includes the acetabular border formed by fusion of the pubic peduncle of the ilium and the proximal pubis (UCMP 25791). Unfortunately the exact association between these additional pieces and the type tibiotarsi is not certain. They should be treated as remains of possibly separate individuals and perhaps different taxa.

Gojirasaurus quayi is known only from an isolated tooth and a few postcranial bones including a scapula, pubis, tibia, and a mid- or posterior dorsal vertebra (Parrish and Carpenter, 1986; Carpenter, 1997). The centrum and arch of the vertebra were not co-ossified at the time of death, and there is no sign of pubis-ilium or tibia-astragalus fusion. Given the results of my ontogenetic analysis, it is likely this individual was at most a sub-adult at the time of death. The incompleteness of the specimen rendered it a 'spoiler' in a phylogenetic pre-test analysis, generating several thousand equally most parsimonious trees and causing a polytomy within the coelophysoid lineage in the strict consensus of those trees. *Gojirasaurus* was found to be as or more derived than *Dilophosaurus*, *Liliensternus*, and *Zupaysaurus* in the 50% majority rule and Adams

consensus trees. The taxon was included in the analysis of Rauhut (2003), and its presence probably contributed to the poor resolution between coelophysoid taxa found in that study.

The type and only specimen of *Procompsognathus triassicus* consists of a partial skeleton that lacks the skull, the cervical and caudal vertebral series, most of the ilia, and the ischia (Fraas 1913, 1914; Ostrom, 1981; Sereno and Wild, 1992; Rauhut and Hungerbühler, 1998). A skull found near the skeleton was originally described as being from the same individual as the postcranial material, but more recent work suggested it was that of a small crocodylomorph archosaur, and not that of a dinosaur (Sereno and Wild, 1992). The postcranial remains preserve several coelophysoid-like features, including broad, triangular dorsal transverse processes, a ventrally downcurved, bowed pubic shaft, and pronounced trochanteric shelf on the proximal femur (Ostrom, 1981; Sereno and Wild, 1992). Earlier reports also suggested the proximal tarsals were fused to each other and to the distal tibia (Sereno and Wild, 1992). The taxon was the sister taxon to *Segisaurus* in some earlier cladistic analyses, and was used as a reference taxon for the clade 'Procompsognathinae' (Sereno, 1997, 1998). The characters used to diagnose 'Procompsognathinae' relative to other coelophysoids have a wider distribution among Coelophysoidea than recognized by previous workers. There was no unambiguous support for a sister-taxon relationship between *Procompsognathus* and *Segisaurus* in my pre-test analyses. The taxon proved highly labile among the other coelophysoids, and it was not included in the main analysis.

Genusaurus sisteronis is a small theropod known from incomplete remains from Early Cretacous (Albian) age sediments of southern France (Accarie et al., 1995). Enough apomorphies are preserved in the material to indicate it was probably more closely related to *Ceratosaurus nasicornis* and the abelisauroids than to the coelophysoids, a result also retrieved by Carrano et al. (2002). The exact position of this taxon relative to the other ceratosauroids remains uncertain. Its inclusion in a pre-test analysis only decreased resolution along the ceratosauroid lineage and generated a large number of equally most parsimonious trees. It was removed from the main analysis.

The enigmatic taxon *Shuvosaurus inexpectatus* was recently incorporated into an extensive analysis of basal theropod relationships (Rauhut, 2003). *Shuvosaurus* was originally identified as a Triassic ornithomimoid (Chatterjee, 1993). The cranial material was redescribed by Rauhut (1997), who concluded *Shuvosaurus* represented a basal theropod of uncertain affinities. A number of features were cited that were regarded to be dinosaur or theropod synapomorphies. These included an inverted 'L'-shaped lacrimal, loss of the postfrontal, and some other features. This unusual taxon was later judged to be a member of the coelophysoid lineage by Rauhut (2003), an unexpected outcome. Its presence in that analysis also had a strong effect upon the position of *Dilophosaurus wetherilli*, contributing to the removal of the latter from Coelophysoidea, placing it closer to tetanuran theropods than to coelophysoids, and requiring a large number of evolutionary reversals among several characters.

The limited published information concerning *Shuvosaurus* was re-evaluated, as well as the character scoring of the taxon by Rauhut (2003). Two characters nested

Shuvosaurus within the coelophysoid lineage in that analysis. They were 1) a forked posterior process on the premaxilla, and 2) an anteroposteriorly elongated basisphenoid. The two posterior processes of the premaxilla in *Shuvosaurus* are different from the medially inset, triangular posteroventral flange at the base of the maxillary process of the premaxilla in *Dilophosaurus* and other coelophysoids. The wording of the character description used by Rauhut (2003) resulted in dissimilar structures being scored together. When the details of the premaxilla-maxilla articulation are addressed separately, it is clear that two different structures were compared. The elongate basisphenoid may or may not be a homologous feature shared by *Shuvosaurus* and derived coelophysoids.

There are doubts as to whether *Shuvosaurus* is a legitimate taxon (Long and Murry, 1995). It is possibile that the specimens in question are chimeras of pseudosuchian and dinosaurian material, given the taphonomy of the quarry from which the type skull of *Shuvosaurus* was collected. I conducted a pre-test phylogenetic analysis that incorporated *Shuvosaurus inexpectatus* as an ingroup taxon. I scored the taxon mostly following Rauhut (2003), but coded approximately a dozen characters different than in that study. These included the previously discussed posterior morphology of the premaxilla, as well as reinterpretation of maxillary morphology and antorbital fenestra/fossa form, among others. My preliminary results found *Shuvosaurus* was the most basal theropod in the analysis, outside an *Eoraptor* + Neotheropoda clade. It shared two unambiguous characters with more derived theropods, an inverted 'L'-shaped lacrimal, and an elongate basisphenoid (lost in most other theropod taxa). The presence of *Shuvosaurus* in the pre-test analysis also resulted in the removal of *Herrerasaurus*

from Theropoda, placing it instead as the most basal saurischian in the analysis outside a *Plateosaurus* + Theropoda clade.

The case for placing *Shuvosaurus inexpectatus* within Theropoda is not strong. The type skull possesses a number of highly autapomorphic features that greatly reduce its utility in basal theropod phylogeny reconstruction. It is unclear from published photos and illustrations what parts of the skull are actually fossil material and what is reconstructed (Chatterjee, 1993; Rauhut, 1997, 2003). The taxon is not included in my main study. The use of *Shuvosaurus* in future analyses of theropod relationships should be avoided until the type skull is subjected to rigorous examination with advanced technologies (such as high-resolution x-ray CT scanning).

A small number of taxa not previously added to analyses of basal theropod or ceratosaurian relationships were included in my study. These included *Aucasaurus garridoi* (Coria et al., 2002), *"Poekilopleuron" valedunensis* (Allain, 2002), the Shake-N-Bake taxon (Tykoski, 1997, 1998), and *Zupaysaurus rougieri* (Arcucci and Coria, 2003). *Zupaysaurus* was described as the earliest tetanuran theropod (Arcucci and Coria, 2003). The claim of tetanuran affinities of the taxon was based upon a limited phylogenetic analysis. Regardless, *Zupaysaurus* is an important taxon because of its temporal (Late Triassic) and geographic (South America) positions, as well as the possibility that it represents a basal member of the tetanuran lineage. The specimen was scored from the literature.

I did not evaluate or include a few taxa purportedly referable to Coelophysoidea. These included *Podokesaurus holyokensis* (Talbot, 1911), incomplete remains named

Syntarsus moenavenisis from the Moenave Formation of Arizona (Lucas and Heckert, 2001), and "*Eucoelophysis baldwini*" (Sullivan and Lucas, 1999). *Podokesaurus holyokensis* was described and named on the basis of an incomplete skeleton discovered in a glacial erratic boulder on the campus of Holyoke College, Massachusetts. The specimen was later destroyed and only a few casts of it remain. The specimen was later assigned to a separate species of *Coelophysis*, *C. holyokensis* (Colbert and Baird, 1958) based upon plesiomorphic similarities shared by the specimen and material referred to *Coelophysis bauri*. I do not recognize the assignment of this specimen to *Coelophysis*. The published figures of the specimen do not lend themselves to effective character state evaluation, and no casts of the specimen were readily available for examination. *Podokesaurus* was therefore left out of the analysis.

"*Eucoelophysis baldwini*" was erected by Sullivan and Lucas (1999) on the basis of an incomplete partial skeleton (NMMNH P-22298) from the Petrified Forest Member of the Chinle Formation. The specimen was found within a few kilometers of the Ghost Ranch (Whitaker Quarry) locality that yielded numerous *Coelophysis bauri* specimens. Thetype specimen of *"Eucoelophysis baldwini"* was reportedly recovered from a stratigraphic horizon below the Ghost Ranch locality. Several anatomical features normally associated with theropod dinosaurs (Gauthier, 1986; Holtz, 1994; 1998; Sereno, 1999; Carrano et al., 2002; Rauhut, 2003) are lacking in the specimen, such as a fibular crest on the lateral surface of the proximal tibia, a posterior notch between the medial and lateral proximal condyles of the tibia, a pronounced cnemial crest extending from the lateral part of the anterior surface of the proximal tibia, a well developed femoral head,

and a sulcus ligament on the posterior surface of the proximal femur creating a hook-like profile of the femoral head in proximal view. Unlike the condition in coelophysoids, the proximal surface of the pubis does not bear two distinct facets set at an angle to one another for receipt of the pubic peduncle of the ilium. The pubic shaft shows little or no anterior convexity, and the distal tip flares laterally, a condition not present in any other coelophysoid.

The material described as "*Eucoelophysis baldwini"* preserves no unambiguous synapomorphies shared with Coelophysoidea. The morphology of the anterior trochanter of the femur bears some resemblance to gracile individuals of *Syntarsus rhodesiensis* and the Shake-N-Bake taxon, but this state may represent a plesiomorphic theropod condition, or may be the result of relative immaturity of the individual. The trochanteric shelf is only a low rounded mound in NMMNH P-22298, contrary to description of Sullivan and Lucas (1999). The metatarsals, described as articulated, are also unusual for a theropod in that the distal articular condyles are all set at approximately the same level (Sullivan and Lucas, 1999:fig. 8). The third metatarsal usually projects well beyond metatarsals II and IV in theropods, and metatarsal IV is usually subequal in length to metatarsal II.

The lack of definitive theropod apomorphies casts doubt upon the assignment of "*Eucoelophysis baldwini*" as a coelophysoid theropod. The type specimen was identified as representing an immature individual (Sullivan and Lucas, 1999). It is then surprising that the authors overlooked the possibility that the material could be that of a young *Coelophysis bauri*. It appears at this time that the only feature that can be used to

differentiate "*Eucoelophysis*" from *Coelophysis* is the lower stratigraphic position of the former. This means that "*Eucoelophysis baldwini*" is diagnosed on the basis of its stratigraphic position, and I do not consider it a valid coelophysoid taxon until specimens with theropod and coelophysoid apomorphies that can be distinguished from *Coelophysis* and other coelophysoids are found and described.

Intersestingly, the two features used by Sullivan and Luca (1999) to diagnose "*Eucoelophysis*" from all other ceratosaurs were the presence of an ischio-acetabular groove on the proximal surface of the pubis, and a distinct sulcus on the proximal surface of the femur. These features are not known in any ceratosaur, but both apomorphies are present in *Saturnalia tupiniquim*, a taxon considered either a member of the sauropodomorph stem-lineage (Langer, 2003, 2004), or a basal prosauropod (Galton and Upchurch, 2004). A sulcus on the proximal femur surface is also present on some poposaurid femora (pers. obs.). This introduces the possibility that the type specimen of "*Eucoelophysis baldwini*" may represent a basal saurischian or stem-sauropodomorph allied with *Saturnalia tupiniquim*.

Character construction and coding

I intended to score the OTUs in this work as consistently as possible with previous analyses. In most cases this was accomplished, but much of the overall character set is coded differently from previous authors. Justifications for scores different from previous authors are dealt with below in discussions of the individual character states. In some cases my interpretation or understanding of a character state

description, and its degree of expression in the specimen was at odds with previous authors' evaluation and scoring. Previous coding was overruled in cases when I was able to examine real fossil material and that material contradicted earlier works. I relied upon published accounts, figures, and illustrations in cases when fossil material could not be personally examined. I then scored differently from previous works only if the anatomy in question was clearly illustrated and in my view was incorrectly interpreted by the previous authors. In cases where the clarity of illustration or description made evaluation difficult, or when specimens were not illustrated, I scored consistent with previous authors. In cases when previous analyses differed in the scores of characters shared between them, the anatomy was evaluated from the specimen or literature and the character coded following my own interpretation of the anatomy

Other characters used by previous workers were reworded and broken up into separate characters if it was determined that more than one independent variable was included in the description. Consider a hypothetical example and the following character: 'Hands with four digits bearing small claws (0), or with three digits bearing large claws (1)'. The wording of the character suggests a relationship between the number of digits and the size of the claws they bear. A new taxon is then discovered that has three digits but small claws. The new taxon immediately presents a condition not encompassed by either option in the character description. The character should not be coded as 'unkown' or 'missing data' for the new taxon, because the true morphology is unequivocally known.

It may be better to erect two new characters from the two potentially independent, variable morphologies in the example above. If the plesiomorphic condition present in the proximal outgroups is four digits that bear small claws, the appropriate wordings of the two new binary characters would be: A) 'Hands with four digits (0), or three digits (1)'; and B) 'Manual digits bear small claws (0), or large claws (1)'. These two separate characters evaluate the presence or absence of two independent, phylogenetically informative character states, and accommodates ingroup taxa with morphologies incompatible with the original wording of the character.

Character List and Descriptions

This section lists all the characters in the phylogenetic analysis. Discussion is provided for characters that are poorly understood, lack clarity of meaning, are potentially contentious, or were scored differently by previous authors. References following character descriptions cite the work in which the particular character was first used (in some form) in a cladistic analysis. Additional references are listed if a character was used or modified in later, more comprehensive cladistic analyses, or if greater illustration of the history of use of the character description is necessary. If no references follow the initial character description, it indicates the character is new. Almost all the character descriptions used by prior authors are rewritten here to some degree. They are written in telegraphic style to facilitate easy transfer in and out of MacClade or other spreadsheet software. In cases where modification to the wording of a character state is substantial, the reference takes the form of, "(modified from author X)".

Much of the scoring of taxa was taken from previous data matrices, but the anatomy was checked using real specimens or the primary literature wherever possible. Table 4 lists all the OTUs in this study, the published works from which each taxon was scored, and the specimens (fossil or casts) personally examined and used to score phylogenetc characters. The complete taxon-character matrix that formed the basis for my analysis is provided in Appendix 4. A digital version of the matrix is available upon request.

Cranial Characters

1. Craniofacial bones (i.e., maxilla, jugal, quadratojugal, nasal) relatively smooth (0), or sculptured (1) (Novas, 1997).

2. Skull length <3 times (0), or >3 times (1) posterior skull height (height = articular condyle of quadrate to dorsal-most edge of parietal) (Forster, 1999; Sereno, 1999a).

This character is scored only in those taxa known from specimens preserving reasonably complete skull material. The character was scored only if the skull was sufficiently known to generate a reasonable, conservative reconstruction of the entire structure (e.g., *Dilophosaurus wetherilli*). Skull length was measured from the anterior-most tip of the premaxilla to the posterior-most margin of the mandibular condyle of the quadrate. Skull height was measured from the ventral surface of the quadrate articular condyle to the surface of the parietal not including the nuchal crest. The size of the nuchal crest can vary greatly among Theropoda, and is especially derived in size and

dorsalward projection in abelisaurids and tyrannosaurids. It would be misleading to include the hypertrophied nuchal crest of abelisaurids in a measurement meant to give a sense of general skull form.

3. Orbit approximately circular (0), or keyhole-shaped, with narrower ventral end (1) (Gauthier, 1986).

4. Orbit anteroposterior diameter > (0), or < (1) internal antorbital fenestra length (Holtz 1998).

5. Internal antorbital fenestra anteroposterior length < 25% (0), or ≥ 25% maximum skull length (Rowe, 1989).

6. Premaxilla body (excludes maxillary and nasal processes) height/length ratio ≤ 1.25 (0), or >1.25 (1) (modified from Holtz 1994, 1998; Sampson et al., 1998; Carrano et al., 2002).

Early incarnations of this character were unclear as to the reference points measured to determine the ratios scored by some previous authors. This may be the cause of inconsistency in the premaxillary height/length ratios between these workers and my own observations. For example, Carrano et al. (2002) scored the premaxilla height/length ratio as "<0.5" in coelophysoid taxa. The wording of the character in that work made reference to measurements of the premaxilla "below naris". It was unclear if

the measurement was taken only directly below the external naris or not. This is especially important to deriving the ratio in coelophysoids, because the external naris is wholly posterior to the main tooth-bearing part of the premaxilla in those taxa. If the measurement is taken ventral to the external naris, only the height of the narrow, rod-like maxillary process is obtained, which gives a ratio of less than 0.5. The problem is that the external naris is positioned dorsal to the main body of the premaxilla in other theropods, and the height/length ratios are derived from vertical measurements through the tallest part of the element. It is not comparable to score ratios of premaxillary body/overall premaxillary length against ratios of maxillary process of premaxilla height/overall premaxillary length.

For this study the premaxillary height/length ratio was obtained by first measuring the vertical distance between the furthest extent of the alveolar border to a plane passing through the ventral-most point of the premaxillary border of the external naris (Fig. 7). This value was then divided by the measurement of the greatest anteroposterior length of the premaxilla. Using this method, almost all coelophysoids have a premaxillary height/length ratio greater than 0.5 and less than 1.25. Exceptions are some specimens of *Syntarsus rhodesiensis* (Raath, 1977). This ratio was scored as ">1.25" in the basal tetanuran *Torvosaurus tanneri* by Carrano et al. (2002). The premaxilla is relatively tall and narrow in this taxon, but my measurements of the premaxillae illustrated by Britt (1991) resulted in a value less than 1.25. The posterior tip of the maxillary process of the premaxilla is incomplete in the specimens figured, which should have resulted in an even higher ratio than was obtained.

7. Premaxilla lateral surface penetrated by many neurovascular foramina (0), or few or none (1).

The lateral surface of the premaxilla is perforated by numerous neurovascular foramina in most theropods. Close examination of premaxillae of *"Syntarsus" kayentakatae* revealed lateral surfaces devoid of neurovascular foramina. A single dimple marks the lateral surface ventral to the base of the nasal process, but it is not clear if this dimple bears a small foramen at its base, or if it is closed (Fig. 8). Raath (1977) described a similar morphology in premaxillae of *S. rhodesiensis*. Photographs and cursory examination of *Coelophysis bauri* material indicate this taxon also lacks premaxillary neurovascular foramina, but it does not bear a dimple near the base of the nasal process (Colbert, 1989). *Eoraptor lunensis* also has a single deep dimple in the premaxilla ventral to the base of the nasal process, and examination of the holotype skull (PVSJ 512) under a microscope failed to reveal other neurovascular foramina in the lateral surface of the premaxilla (pers. obs.).

8. Premaxilla nasal process comprises > 50% (0), or ≤ 50% (1) of external naris anterodorsal border (Holtz, 1998).

The nasal process (=dorsal process) of the premaxilla is laterally overlapped by an anterior process of the nasal in most theropod taxa. The right and left premaxillary nasal processes are therefore clasped by the nasals, forming the internarial bar. Determination of the percentage of the narial border rimmed by premaxillary nasal process was based

upon the part of the nasal process visible only in lateral view. This is consistent with the scoring and results obtained in earlier analyses, but it is acknowledged that some amount of the premaxillary nasal process continues posterodorsally between the nasals.

9. Premaxillary tooth row terminates ventral to (0), or entirely anterior to (1) external naris (Sereno, 1999a).

The anterior border of the external naris is positioned dorsal to the premaxillary tooth row and over the dorsoventrally tallest part of the premaxilla in most basal theropods. The external naris is shifted far posteriorly in *Dilophosaurus wetherilli*, *Coelophysis bauri*, *"Syntarsus" kayentakatae*, *Syntarsus rhodesiensis*, *Baryonx walkeri*, and *Suchomimus tenerensis* so that the anterior rim of the opening is even with or posterior to the margin of the last premaxillary tooth (Figs. 7-10). The degree of naris posterior displacement in *Baryonyx* and *Suchomimus* is such that the rim of the opening is far posterior to the last premaxillary tooth. This is unlike the condition in *D. wetherilli* and the other coelophysoids in which the rim of the naris is only slightly posterior to the last premaxillary tooth.

10. Premaxillary lateral surface dorsal to second tooth position smooth (0), or marked by small pit at base of nasal process (1).

See Figure 8 and discussion of character seven above.

11. Maxillary process of premaxilla dorsoventrally wide and plate-like (0), or narrow and rod-like (modified from Gauthier, 1986; Rauhut, 2003).

Rauhut (2003) correctly noted that the form of the maxillary process of the premaxilla of saurischians differs from the condition in Ornithischia and less derived archosaurs. The character as described in that work incorporated two potentially independent features, which I treat as two discrete, binary characters (see below).

12. Maxillary process of premaxilla contacts nasal (0), or does not contact nasal, allowing maxilla to contribute to rim of external naris (1) (modified from Gauthier, 1986; Holtz, 1998; Rauhut, 2003).

This character is difficult to evaluate in all but the best-preserved skulls. The anterior tip of the nasal bone is a delicate structure that does not preserve well. Also, the maxillary process of the premaxilla and the nasal do not line up in an abutting relationship below the external naris. Instead, the nasal may be slightly lateral to the premaxilla's maxillary process. The nasal and maxillary process of the premaxilla contact or overlap in the ornithischians *Lesothosaurus* and *Scutellosaurus*, *Herrerasaurus*, *Eoraptor*, *Allosaurus*, and *Ornitholestes*. The elements do not contact or overlap in *Dilophosaurus* (UCMP 77270), *Coelophysis* (AMNH 7224), and reportedly not in *Syntarsus rhodesiensis* (Raath, 1977). The anterior end of the left nasal is displaced and rotated in the type skull of *"Syntarsus" kayentakatae*, but it is unlikely there was any contact or overlap between the two elements in this taxon. There is no

contact between the two in *Ceratosaurus*, the abelisaurids *Carnotaurus* and *Majungatholus*, spinosaurids, or *Eustreptospondylus*.

13. Maxillary process of premaxilla anteroposterior length ≥ (0), or much < (1) length of alveolar body of premaxilla (modified from Holtz, 1998).

14. Maxillary process of premaxilla ventral margin unexpanded (0), or with posteroventrally directed flange, resulting in appearance of "forked" premaxilla: (Rauhut, 2003).

The presence of a posteriorly directed process on the premaxilla ventral to the maxillary process in *Syntarsus*, *Coelophysis*, the tetanuran *Compsognathus*, and the enigmatic taxon *Shuvosaurus* was noted by Rauhut (2003). This feature in *Shuvosaurus* was a factor in establishing the coelophysoid affinities of the taxon in Rauhut's (2003) hypothesis. A premaxilla of *Syntarsus rhodesiensis* bearing an extremely long, rod-like secondary process that gave the premaxilla a truly forked maxillary articulation was figured by Rauhut (2003:fig. 8) (Fig. 9A). The long embayment between the two processes evidently received the anterior process of the maxilla. It is assumed that the unusual structure in this particular specimen is what led Rauhut (2003) to judge this character absent in *Dilophosaurus*, reducing support for the taxon's inclusion with the coelophysoids.

The premaxilla illustrated by Rauhut differs greatly from previous descriptions. Only a small triangular flange projected posteroventrally from the base of the maxillary

process in original descriptions and illustrations of *Syntarsus rhodesiensis* premaxillae (Raath, 1977). I cannot fully account for the exceptionally long ventral process in the premaxilla figured by Rauhut (2003). However, close examination of the image provided by Rauhut (2003:fig. 8) reveals a possible explanation. The anterior part of the ventral process in the figured specimen has the form of a posteroventral, triangular flange. A break separates the flange-like part of the process from the rod-like and posteriorly directed part of the structure. Also, there is a difference in color and texture of the bone across the break. It is possible that another piece of bone is cemented to the posteroventral flange of the specimen. This is of course speculative until the specimen is examined.

The presence of a posteroventral flange on the maxillary process of the premaxilla is not visible in the type skull of *"Syntarsus" kayentakatae* (MNA V2623). A badly weathered paratype skull (also numbered MNA V2623) from the same quarry as the type has a disarticulated right premaxilla exposed in medial view (Fig 9B). The premaxilla bears a posteroventral flange matching the morphology originally described in *Syntarsus rhodesiensis*. The flange is much shorter in length than the maxillary process, and tapers to a sharp terminus. A triangular fossa is present on the medial surface of the flange, with the narrow apex of the fossa pointing anteriorly and slightly dorsally into the juncture of the maxillary process and the posteroventral flange.

The premaxilla of *Dilophosarus* also bears a posteroventral flange descending ventrally and medially from the base of the maxillary process (contra Rauhut, 2003). The flange is broken and not entirely preserved, but its base is clearly present on the left

premaxilla of UCMP 37303 (Fig 9C). A shallow fossa excavates the flange's medial surface, just as in the referred specimen of *"Syntarsus" kayentakatae*. The premaxilla of another skull referred to *D. wetherilli* (UCMP 77270) is poorly preserved, but also has remnants of the flange. The premaxilla of *Coelophysis bauri* has a structure similar to *"Syntarsus" kayentakatae* (Colbert, 1989). The shared presence of this morphology in these taxa refutes the claim (Rauhut, 2003) that the premaxilla-maxilla articulation in *Dilophosaurus wetherilli* is more like that of spinosaurids than other coelophysoids.

15. Palatal process of premaxilla a pronounced shelf (0), or only a blunt ridge or absent (1) (Sampson et al., 1998).

16. Premaxilla and maxilla with strong, immobile articulation (0), or are only loosely articulated with each other (1) (Tykoski, 1998; Sereno, 1999a).

The possibility of a loose or potentially kinetic contact between the premaxilla and maxilla in various coelophysoid taxa was mentioned in a number of papers on these taxa (Raath, 1977; Welles, 1984; Colbert, 1989; Rowe et al., 1997). The anatomical details of the articulation were only generally described, and were never figured. Specimens of *"Syntarsus" kayentakatae* and *D. wetherilli* provide an opportunity to describe and illustrate this coelophysoid feature in both disarticulated and articulated material.

The major structural feature that facilitates potential mobility between the two elements is the loss of a lateral contact between the premaxilla and maxilla (Fig. 10A).

The maxillary process of the premaxilla is inset medially from the lateral surface of the premaxillary body, that portion of the premaxilla that bears the alveoli. The resulting space between the lateral surfaces of the premaxilla and maxilla was termed the "subnarial gap" (Welles, 1984). The maxillary process is about equal to the length of the premaxillary body, and as discussed earlier it bears a triangular flange at its base (Fig 9). The medial surface of this flange bears a fossa that receives the anteromedial process of the maxilla. The anteromedial process of the maxilla is a long, finger-like projection.

The maxillary process of the premaxilla lies in an elongate groove along the dorsal surface of the maxillary anterior process (=premaxillary process, =rostral process of Carrano et al., 2002) (Fig. 10B,C). A deep notch separates the lateral surface of the maxillary anterior process from the maxilla's anteromedial process. The posteroventral flange of the premaxilla's maxillary process slides into the notch, and the dorsal, rod-like component of the maxillary process rests in the groove on the dorsal surface of the maxillary anterior process (Fig. 10C). The anteromedial process of the maxilla projects to a point near the base of the premaxilla's maxillary process when naturally articulated.

Contact between the premaxilla and maxilla occurs at only three places in coelophysoids known from adequate material. The first is the contact between the medial fossa on the premaxilla's posteroventral flange and the maxilla's anteromedial process (Fig. 9B). The second contact is between the ventral surface of the premaxilla's maxillary process and the dorsal groove along the maxilla's anterior process (Fig. 10B). The third is the contact between the premaxilla's posteroventral flange and the anterior surfaces of the maxilla's anterior process. All the surfaces of the elements in question are

smooth, with no sign of interdigitation or suturing. In other theropods the premaxilla and maxilla meet along a broad abutting contact as well as along the interface between the premaxilla's maxillary process and the maxilla's anterior process. I concur with earlier suggestions that the premaxilla-maxilla articulation in coelophysoids was likely kinetic.

This unique morphology is present in specimens of *Dilophosaurus*, *Coelophysis*, *"Syntarsus" kayentakatae*, and *Syntarsus rhodesiensis*. Other coelophysoid taxa are not represented by cranial material that preserves this region. The morphology of the premaxilla-maxilla contact in the cranial reconstruction of *Shuvosaurus inexpectatus* is very different from that described above. There is no subnarial gap (contra Chatterjee, 1993; Rauhut, 2003), and there is no evidence for the loose, three-point contact between the premaxilla and maxilla seen in the coelophysoids. It is interesting to note that both premaxillae of the type skull of *Zupaysaurus* were not attached to the maxillae of the specimen, and were not recovered. This may hint at the presence of a loose, coelophysoid-style articulation for the premaxilla in this taxon.

17. Premaxilla and maxilla in contact at alveolar margins (0), or alveolar margins do not contact (1).

This character represents a rewording of the concept of the subnarial gap mentioned in discussion above. The "subnarial gap" (Welles, 1984) was never adequately defined as an anatomical feature, and later it was loosely applied to any diastema or interruption of the alveolar margin at the premaxilla-maxilla juncture. I

concentrate on a description that recognizes the relationship of osseous elements that incidently result in the subnarial gap.

The alveolar margins of the premaxilla and maxilla do not meet in *Dilophosaurus*, *Coelophysis*, *S. rhodesiensis*, and *"S." kayentakatae*, as explained above (Figs. 8A, C). This feature cannot be assessed in other coelophysoid taxa, because they lack the pertinent cranial material. This is also the case for *Elaphrosaurus bambergi*, a taxon with many coelophysoid-like features in its postcranial skeleton. The lack of a lateral or alveolar contact between the premaxilla and maxilla is not in itself an indication of a loose or kinetic union. For example, a large notch at this juncture breaks the alveolar border of many crocodylomorph taxa, yet there is an exceptionally rigid connection between these elements in most crocodylomorphs.

The derived state of this character is not present in the spinosaurids *Baryonyx walkeri* and *Suchomimus tenerensis*. The alveolar borders of the premaxilla and maxilla each pinch dorsally at their common juncture. The lateral surfaces of the bones and their alveolar borders are continuous across the contact, unlike the condition among coelophysoids.

18. Premaxilla-maxilla suture uninterrupted (0), or interrupted by subnarial foramen (1) (Gauthier 1986, Novas, 1992; Sereno et al., 1993; Coria and Salgado, 1998).

The subnarial foramen is present in *Herrerasaurus*, *Plateosaurus* and other basal sauropodomorphs, *Eoraptor*, and some tetanuran clades. It is absent in the coelophysoids, *Ceratosaurus*, abelisaurids, the spinosaurids *Baryonyx* and *Suchomimus*,

and *Ornitholestes*. The distribution of this feature among other basal tetanurans is not clear. Even in many taxa for which cranial material is known (e.g., *Torvosaurus tanneri*, *"Poekilopleuron" valedunensis*) the preservation along the premaxilla-maxilla margin is not adequate to unambiguously demonstrate the existence of this small foramen.

19. Anterodorsal margin of maxilla is linear or anterodorsally convex (0), or anterodorsally concave (1) in lateral view (modified from Holtz, 1998).

This and the following five characters (19-26) serve to encompass the highly variable morphology of the anterior part of the maxilla among basal theropods. Numerous attempts were made by previous authors to score the morphology of the anterior maxilla, but the character descriptions and options suffered from incorporating many independent variables within a single description (Holtz, 1998; Carrano et al., 2002; Rauhut, 2003). I attempted to identify and isolate as many variable factors in the form of the theropod anterior maxilla as possible in these nine characters.

The anterodorsal border of the maxilla is defined here as the edge extending posterodorsally from the anterior tip of the alveolar margin to either the tip of the maxillary dorsal process (=posterodorsal process, =nasal process, =ascending process), or to the first major angular change in the posterodorsal orientation of the maxillary dorsal process. Any degree of posteroventral bowing of this margin in lateral view is scored as a concave anterodorsal border. This border is convex anterodorsally in *Herrerasaurus* (discounting the presence of an autapomorphic foramen along the maxilla/premaxilla margin), almost straight in *Lesothosaurus*, but concave in *Plateosaurus*, *Eoraptor*, and all

the other theropods in this study known from adequate material (Fig. 11). Even the very steep anterodorsal maxillary margin in *Carnotaurus* is faintly concave in lateral view.

20. Transition along dorsal border of maxilla from anterior process to dorsal process is gradual, smoothly curved (0), or abrupt to angular (1) in lateral view.

It is important to define boundaries for the dorsal process of the maxilla, and the anterior process of the maxilla. The anterior limit of the dorsal process is marked at the first noticeable dorsal inflection of the anterodorsal border of the maxilla (Fig. 12A). The posterior margin of the dorsal process' base is marked at the first posterior inflection of the posterior margin of the process where it rejoins the alveolar body of the maxilla. The anterior process of the maxilla is bounded anteriorly by its anterior tip, and posteriorly by a transverse plane passing through the same inflection point marking the rise of the dorsal process of the maxilla (Fig. 12A).

The transition at the boundary-defining inflection point on the maxilla's anterodorsal border can be gradual (Fig. 12B), or it can be relatively abrupt with a kink or obvious angular difference between the two processes (Fig. 12C). The inflection between the anterior and dorsal processes is effectively indiscernable in *Lesothosaurus* and *Herrerasaurus*, and gradual in *Eoraptor*, *Coelophysis*, *Syntarsus rhodesiensis*, *Ceratosaurus*, abelisauroids, *Irritator*, *Suchomimus*, and *Allosaurus*. A gradual, smooth transition is therefore the primitive state among the taxa tested. The state of the feature is not known in *Marasuchus*, *Scutellosaurus*, and a number of the remaining theropods in this study.

The angle of inflection between the anterior and dorsal processes of the maxilla is angular and abrupt in *Plateosaurus* and many other basal sauropodomorphs, although it is not clear what morphology was present in the most basal sauropodomorphs (Galton, 1984b, 2001; Galton and Upchurch, 2004). *Torvosaurus* and "*Poekilopleuron*" *valedunensis* each exhibit strongly offset dorsal processes among the tetanurans in the analysis. The dorsal process of the maxilla of *"Syntarsus" kayentakatae* differs markedly from *Syntarsus rhodesiensis* and *Coelophysis* by rising sharply from a small anterior process of the maxilla (Fig. 12B, C).

The situation for *Dilophosaurus* is complicated. A distinct anterior process of the maxilla was scored as absent in the taxon by Holtz (1998), who considered the anterodorsal surface of the maxilla to be convex and continuous from the ventral margin of the bone to the tip of the dorsal process. This evaluation was echoed by Carrano et al. (2002) who also scored the anterior process as "absent/small" in that analysis. I believe previous workers were misled by poor preservation of this part in the maxillae of UCMP 37303. The drastically upturned anterior tip of the maxilla in this taxon makes it appear as if there is no anterior process of the maxilla.

The anterior part of the maxillary dorsal process is missing in both maxillae of UCMP 37303 (Fig. 13A, B). The dorsal process is also missing in TMM 43646-1. Based on these specimens alone this character (and the preceding character) cannot be evaluated for the taxon, because part of the anatomy of interest is not preserved. Luckily, this area is well preserved in UCMP 77270. There is a kink and obtuse angle marking the rise of the dorsal process, and the anterodorsal margin of the maxilla is subsequently

concave in lateral view. The area anterior to the kink is the anterior process. The dorsal margin of the anterior process curves anteroventrally until it meets the alveolar margin which itself curves anterodorsally. The anterior process of *Dilophosaurus* therefore has two convex-outward margins that meet to form a point (Fig. 11D, 13C).

21. Dorsal process of maxilla axis angles posterodorsally between 35º and 50º (0), or ≤ 35º (1), or >50º (2) from horizontal. (UO)

The axis of the maxillary dorsal process is measured here by first setting the alveolar row as horizontal as possible. A horizontal line is then projected through the concave inflection point along the anterodorsal margin of the maxilla. A point corrsponding to the horizontal center of the dorsal process is located. A second line is then drawn from the selected centerpoint, and projected through the center of mass of the dorsal process, using a 'best fit' method (Fig 14A). When this is done, the dorsal process of most basal theropods angles posterodorsally between 35º and 50º from horizontal (Fig. 14A).

The axis of the dorsal process of the maxilla rises at an angle greater than or equal to 50º from horizontal in *Abelisaurus*, *Carnotaurus*, *Majungatholus*, *Masiakasaurus*, and *Noasaurus* (Fig. 14B-F). It appears that it also does in the recently described abelisaurid *Aucasaurus*, but an adequate cranial description of this taxon is not yet published (Coria et al., 2001). The maxilla is not known in the basal abelisaurid *Ilokelesia*, or in *Xenotarsosaurus*. Lamanna et al., (2002) described an abelisaurid maxilla from a site

very near the type locality of *Xenotarsosaurus*. It bears a very steep dorsal process similar to the condition in *Carnotaurus*.

The dorsal process of the maxilla angles posterodorsally less than 35º from horizontal in the coelophysoids *Coelophysis* and *Syntarsus rhodesiensis* (Fig. 14G). Some specimens of each taxon, particularly ontogenetically less developed individuals, tend to have a shorter, deeper rostrum than their larger counterparts (Colbert, 1989; figs. 29, 35). This manifests itself in part by possession of a steeper dorsal process on the maxilla. The expression of this character might be influenced by taphonomy and the condition of individual specimens. The true morphology of the dorsal process may be individually variable among adult specimens of these taxa. The type skull of *"Syntarsus" kayentakatae* (MNA V2623) and a skull referred to *Dilophosaurus* (UCMP 77270) each have steeper dorsal processes, with axes between 35º and 50º.

22. Dorsal process of maxilla long and contacts lacrimal (0), or with very short posterior component that does not contact lacrimal (1) (Coria et al., 2002).

The dorsal process of the maxilla of most theropods extends posterodorsally to contact the anterior process of the lacrimal. The two elements then serve to form the upper margin of the internal antorbital fenestra, and usually bear respective parts of the external antorbital fenestra on their lateral surfaces. The relative proportions of the contribution made to the upper margin of the fenestra varies among taxa. The abelisaurids *Aucasaurus*, *Abelisaurus*, *Carnotaurus*, and *Majungatholus* are unusual in that the dorsal process is dorsoventrally tall, but has little or no posterior extension (Fig.

15A, B). It also has no contact with the lacrimal above the internal antorbital fenestra, which is then bordered dorsally by the nasal. The morphology of the process in *Ilokelesia* is not known.

23. Anterior process of maxilla length ≤10% (0), or 10% < 25% (1), or ≥ 25% (2) total maxilla length. (UO)

The length of the anterior process of the maxilla is a very small percentage (≤10%) of total maxilla length in *Lesothosaurus*, *Herrerasaurus*, *Eoraptor*, *"Syntarsus" kayentakatae*, *Coelophysis*, *Syntarsus rhodesiensis*, *Carnotaurus*, and *Noasaurus* (Fig. 16A). The anterior process constitutes a greater percentage of maxilla length in *Plateosaurus* and other basal sauropodomorphs, as well as most other theropods. This and the following character represent arbitrary, albeit clustered divisions of the potentially continuous spectrum found in the length of the anterior process relative to the entire maxilla. The anterior process of the maxilla is between 10 and 25% total maxilla length in *Plateosaurus*, *Dilophosaurus*, *Ceratosaurus*, *Abelisaurus*, *Majungatholus*, possibly *Masiakasaurus*, and *Allosaurus* among taxa in this analysis (Fig 16B). Only a few theropod taxa have an anterior process of the maxilla that is greater than 25% total maxilla length (Fig. 16C). The basal tetanurans *Torvosaurus*, *Eustreptospondylus*, *"Poekilopleuron" valedunensis*, *Irritator*, and *Suchomimus* exhibit this character state in this analysis. The material of *Baryonyx* does not preserve the enough of the maxilla to establish the percentage the anterior process represents of total maxilla length.

24. Ratio of dorsoventral height of proximal end of anterior process of maxilla versus height of alveolar ramus of maxilla at first alveolus posterior to rim of internal antorbital fenestra <1.0 (0), or ≥1.0 (1).

This character establishes reference points by which the dorsoventral height of the anterior process of the maxilla can be evaluated relative to the more posterior part of the element. Previous works qualified the size of the anterior process, but they were either highly subjective (i.e., "anterior process absent /small"), or they compared the height of the process to its own length, which might not be independent (Sereno et al., 1996; Holz, 1998; Caranno et al., 2002). The metric devised here seeks to provide a more reproducible and testable means of evaluating whether a maxillary anterior process is dorsoventrally tall or short relative to the rest of the maxilla.

The ratio derived from these measurements is achieved by dividing the measurements of the dorsoventral height of the maxilla at two points. The first point is at the proximal end of the maxillary anterior process, at the inflection point marking the transition from the anterior process to the dorsal process of the maxilla (Fig. 17A). The second point is at the plane through the first poaterior edge of the first alveolus that is completely posterior to the anterior rim of the internal antorbital fenestra (Fig. 17A). The reason for taking the measurement here instead of at the posterior inflection point of the maxillary dorsal process is that the anteroventral rim of the internal antorbital fenestra usually curves posteroventrally in theropods. The maxilla is therefore still relatively tall directly under the anterior edge of the fenestra. A measurement taken at a slightly more

posterior position along the alveolar ramus is a better gauge of the dorsoventral height of the maxilla posteror to the dorsal process.

The ratio derived from these measurements is greater than 1.0 in *Herrerasaurus*, but less than 1.0 in *Plateosaurus* and *Eoraptor* (Fig. 17A). The ratio is greater than 1.0 in most of the other theropods in this study for whichi this part of the skull is known (Fig. 17B), except for *"Syntarsus" kayentakatae* and *Noasaurus*, and perhaps some specimens of *Syntarsus rhodesiensis* (Fig. 17C). The form of the maxillary anterior process in *"Syntarsus" kayentakatae* is apomorphic in that it is sharply set off from the dorsal process as in some basal tetanurans, yet it is also dorsoventrally very short and comprises much less than 10% of the length of the maxilla.

25. Anterior tip of maxillary alveolar margin oriented approximately horizontal (0), or curves sharply mediodorsally (1) (modified from Rowe, 1989).

Rowe (1989) erected this character in recognition of the strongly upcurved anterior tip of the maxilla in *Dilophosaurus*, *Coelophysis*, *"Syntarsus" kayentakatae*, and *Syntarsus rhodesiensis*. What was not fully noted then was that the anterior tip of the maxilla curves dorsally and medially. This is visible in the articulated premaxilla and maxilla in the type of *"Syntarsus" kayentakatae* (MNA V2623), as well as in maxillae of *Dilophosaurus* (UCMP 337303, 77270) (Fig. 18A-C). The anterior end of the maxilla also curves sharply dorsally in the spinosaurids *Baryonyx* and *Suchomimus*.

26. Maxillary first alveolus opens ventrally (0), or anteroventrally (1) (Rowe, 1989).

This character was not included most of the analyses of basal theropod relationship after its use by Rowe (1989) and Rowe and Gauthier (1990). It is possible that subsequent workers considered the anteroventral orientation of the first maxillary tooth to be dependent upon the anterodorsally upturned anterior end of the maxilla in these taxa. However, the first maxillary alveolus in *Masiakasaurus* is also oriented anteroventrally. The single maxilla known for this taxon is missing its anteroventral tip, but it does not bear any sign that the alveolar margin curves dorsally at the second alveolus, a feature present in the coelophysoids listed above (Fig. 18A-C). This suggests that an anteroventral orientation for the first maxillary tooth is not strictly dependent upon a dorsal-ward curvature of the maxilla's anterior alveolar margin, and therefore it should be treated for the time being as an independent character.

27. Maxilla with <20 (0), or ≥20 (1) teeth/alveoli in adults.

There does appear to be a notable difference in the number of maxillary teeth found in derived coelophysids versus the number present in most theropod outgroups, *Dilophosaurus*, *Ceratosaurus*, abelisaurids, and most tetanurans. There are 18 maxillary teeth restored in *Herrerasaurus*, and the same number in the type skull of *Eoraptor*. *Lesothosaurus* was most recently restored with approximately 15 maxillary teeth (Sereno, 1991). *Plateosaurus* bears upwards of 25 maxillary teeth, but the number present in other basal sauropodomorph taxa is highly variable, ranging from as few as 11 to as many as 30 (Galton, 1990). It should be noted that the number of maxillary teeth in basal sauropodomorphs may increase through ontogeny (Galton, 1990), which could effect

some of the published maxillary tooth counts. *Plateosaurus* is known from multiple individuals of various sizes (and assumed ontogenetic stage) which allow a more confident evaluation of the number of maxillary teeth in adults of the taxon.

Carrano et al. (2002) used the character, "maxillary tooth count: >(0) or ≤ (1) 17" to emphasize the morphological distinction between *Eoraptor*, *Herrerasaurus*, and coelophysoids (minus *Dilophosaurus*), and *Dilophosaurus* and all other theropods in their study. The selection of 17 teeth as the 'magic number' may reflect a priori assumption of theropod phylogeny. As noted above, *Herrerasaurus* and *Eoraptor* each reportedly have 18 maxillary teeth, and a character state division drawn just one fewer than this serves only to emphasize the gap between these taxa and more derived theropods. It makes more sense to focus on a more obvious morphological gap if the number of maxillary teeth will be used as a phylogenetic character.

The maxilla of adult *Coelophysis* bears from 22 to 26 alveoli as reported by Colbert (1989), and 19-20 were thought present in *Syntarsus rhodesiensis* (Raath, 1977). There are 20 maxillary tooth positions in the type skull of *"Syntarsus" kayentakatae* (MNA V2623), two more than originally reported (Rowe, 1989). All the other theropods in this analysis for which adequate material is known bear 17 or fewer maxillary teeth, with the exception of the spinosaurid *Suchomimus*, which has 22 maxillary teeth (Sereno et al., 1998). It is clear that these taxa have an unusually high number of maxillary teeth among theropods, which is scored here as a discrete character.

28. Maxilla with >10 (0), ≤10 teeth/alveoli in adults (modified from Carrano et al., 2002).

Most non-avian theropods bear at least 11-12 teeth in the maxilla. *Noasaurus leali* is unusual in that the maxilla has only 10 tooth positions. The maxilla of *Masiakasaurus knopfleri* is incomplete posteriorly, but retains parts of at least seven alveoli in the preserved portion of the element. If the posterior end of the maxillary alveolar ramus retained normal theropod proportions it is unlikely that there were more than two or three additional alveoli in the complete maxilla (Carrano et al., 2002). I tentatively include this character in the analysis. I acknowledge that these two Gondwanan taxa are very small theropods, and that maxillary tooth count may be effected by overall size and the ontogenetic stage of the individual.

29. Maxillary tooth row ends posterior or ventral (0), or anterior (1) to anterior rim of orbit (Gauthier 1986).

This character has persisted since its use in the first cladistic test of saurischian phylogeny (Gauthier, 1986). It was recently rewritten as an ordered multi-state character that further differentiated the exact termination point of the maxillary tooth row as being near the halfway point of the orbit (Fig. 19A), or at the anterior rim of the orbit (Fig. 15A), or wholly anterior to the lacrimal (Fig. 19B) (Rauhut, 2003). This character does not warrant further breakdown of the position of the tooth row terminus.

First, there appears to be a relationship between those taxa Rauhut (2003) scores as having the proposed intermediate character state (terminus under anterior edge of

orbit) and an anteroposterior narrowing of the orbital opening. The keyhole-shaped orbit of these taxa may not have an effect upon the termination point the tooth row itself, but instead it may simply shift the rim of the orbit in a relatively posterior direction (Fig. 19B). All the taxa that retain the primitive condition of the tooth row terminus approximately halfway under the orbit also have large, near-circular orbits (Fig 19A).

Second, the appraisal of the proposed intermediate state depends upon the orientation of the skull when viewed by the evaluator. For example, the last alveolus lies well posterior to the anterior rim of the orbit when the skull of *Carnotaurus* is rotated to bring the tooth row and quadrate into a nearly horizontal plane (Fig 19C). I adopted this orientation when evaluating the other theropod skulls for this character. *Carnotaurus* should be therefore be scored the same as more basal taxa such as *Herrerasaurus*, *Eoraptor*, *Coelophysis*, and *Syntarsus* with regards to this character, following the criteria of Rauhut (2003). Unfortunately, the compound OTU 'Abelisauridae' was used in that analysis, and the group as a whole is scored as having the terminus below the anterior rim of the orbit. It does appear that the last alveolus of *Majungatholus* lies ventral to the orbital rim (Sampson et al., 1998; Fig. 15A).

Holtz (1998) and Carrano et al. (2002) scored the tooth row in *Dilophosaurus* as terminating anterior to the orbit. Rauhut (2003) scored this taxon as having the intermediate condition of the tooth row terminating below the anterior rim of the orbit. The anterior half of the maxilla is missing in the type of *Dilophosaurus wetherilli* (UCMP 37302), and the posterior extremities are missing from both maxillae of the referred paratype (UCMP 37303) (Fig. 13A, B). There are alveoli for 12 maxillary teeth

in the preserved portions of the paratype, and it appears that the posterior teeth in the holotype were numbered in accordance with the preserved portions of the paratype. The left lacrimal of the holotype skull is also displaced posteriorly (Fig. 20A, B), further distorting reconstructions that show the tooth row terminating anterior to the orbit.

It must be remembered that these two specimens represent remains of young individuals of the taxon. As with prosauropods and other coelophysoids (Colbert, 1989) it is possible there was an increase in the maxillary tooth count through ontogeny. UCMP 77270 is a more ontogenetically advanced individual, and it bears 14 teeth in the complete right maxilla. When the skull of UCMP 77270 is oriented with the tooth row near horizontal, the last alveolus is positioned under the anterior half of the orbit, well posterior to the lacrimal (Fig. 11F).

30. Ventral margin of maxillary antorbital fossa indistinct or marked by low rounded ridge (0), or sharply marked by alveolar ridge that parallels alveolar margin (1) (Rowe, 1989; Rowe and Gauthier, 1990).

Rowe (1989) first noted the shared presence of this feature in several theropod taxa, and labeled it the alveolar ridge. Whereas the ventral margin of the external antorbital fenestra (sensu Witmer, 1997) in theropods is usually marked only by a low rounded ridge or textural change in maxilla's surface bone, there is a stark, rounded longitudinal ridge paralleling the alveolar margin in some coelophysoid taxa. These include *Liliensternus*, *Coelophysis*, *"Syntarsus" kayentakatae*, *Syntarsus rhodesiensis*, and the Shake-N-Bake taxon. The feature was described as merely a "pronounced"

ventral rim on the antorbital fossa, and coded as an "anteroventral border of antorbital fenestra demarcated by raised ridge" by Carrano et al., (2002:532). They also pointed out that there is also a sharp ventral margin to the antorbital fossa in *Eoraptor*, *Noasaurus*, *Masiakasaurus*, and *Ornitholestes*.

The alveolar ridge is not as simple a structure as its use in the work above suggests, and it may not be homologous to the relatively sharp ventral rim of the antorbital fossa in some or all the taxa listed by Carrano et al. (2002). The maxillary antorbital fossa (Witmer, 1997) of basal theropods is usually manifested as a broad, relatively shallow depression that is medially inset from the lateral surface of the maxilla. The ventral margin of the fossa often dips in a posteroventral direction across the maxilla in many taxa (e.g., *Dilophosaurus*, *Carnotaurus*, *Allosaurus*). In other words, if the axes of the fossa's ventral rim and the alveolar margin of the maxilla were continued posteriorly, they would typically intersect a short distance past the actual posterior terminus of the maxilla (Fig. 21A).

The alveolar ridge (sensu Rowe, 1989) differs from the normal theropod pattern in that the ridge is actually a lateral extension of the antorbital fossa itself. Transverse cross-sections obtained by CT scanning the skull of MNA V2623 (*"S." kayentakatae*) confirm that the alveolar ridge is asymmetrical for most of its length. In cross-section, the surface of the maxilla traces a gentle slope ventrolaterally towards the alveolar ridge (Fig. 21B,C). The ridge itself is barely discernable from the surface of the fossa. The profile of the maxilla on the ventral side of the ridge cuts sharply in the medial direction, slightly undercutting the alveolar ridge and maxillary antorbital fossa. A small span of

the maxilla separates the alveolar ridge from the ventral margin of the bone. The narrow span of the maxilla ventral to the alveolar ridge is inset medially from the surface of the antorbital fossa dorsal to the alveolar ridge, the opposite of the condition normally present in Theropoda.

The alveolar ridge in these coelophysoids also differs from the normal theropod condition in that the axis of the ridge effectively parallels the alveolar margin of the maxilla (Fig. 21D). Axes drawn through the alveolar ridge and the ventral margin of the maxilla would intersect a great distance posterior to the skull, if at all. The alveolar ridge is also visible all the way to the posterior extremity of the maxilla in the type skull of *"Syntarsus" kayentakatae*, where it seems to be continued there as a strong longitudinal ridge on the jugal. At this time the posterior extent of the ridge is not certain in *Liliensternus*, *Coelophysis*, *Syntarsus rhodesiensis*, and the Shake-N-Bake taxon.

It is unknown at the present time if the ventral rim of the antorbital fossa in the non-coelophysoid taxa listed by Carrano et al. (2002) resembles the condition present in *"Syntarsus" kayentakatae*. The maxilla of *Eoraptor* bears an alveolar ridge similar to that in *"S." kayentakatae* (pers. obs). It is difficult to tell from the photograph of the maxilla of *Masiaksaurus* (Carrano et al., 2002:fig. 2A) if the pronounced ventral rim of the antorbital fossa in that taxon is undercut ventrally, and if the maxilla is medially inset ventral to the rim of the antorbital fossa. The same is true of the maxillae of *Noasaurus* and *Ornitholestes*. It is clear though that the ventral rim of the maxillary antorbital fossa slopes posteroventrally in both of the latter taxa. The antorbital fossa may parallel the alveolar margin in *Masiaksaurus*.

I treat the alveolar ridge present in certain coelophysoid theropods as a uniquely derived structure. It represents either the dorsal margin of a medially inset lateral maxillary surface ventral to the antorbital fossa, or the ventral margin of a laterally projected antorbital fossa that dorsally overhangs the alveolar margin of the maxilla. The fact that it parallels the alveolar margin may be an independent character in its own right, but at this time I do not split this component of its morphology into a separate discrete character. I score this feature as absent in *Masiakasaurus*, *Noasaurus*, and *Ornitholestes* until the relationships between the ventral rim of the maxillary antorbital fossa and the lateral surface of the maxilla ventral to it are shown to match the condition in these coelophysoids. I tentatively code the character as present in *Eoraptor*, pending further examination of the skull and a CT cross-section through the rostrum.

31. Maxillary antorbital fossa anterior to internal antorbital fenestra broad (0), or narrow, extends little beyond rim of internal antorbital fenestra (1) (Sereno et al., 1994; Forster, 1999).

32. Anterior margin of maxillary antorbital fossa rounded (0), or squared, with angular corners and nearly straight anterior border (1) (Rauhut, 2003).

33. Maxillary antorbital fossa ventral to internal antorbital fenestra broad (0), or very narrow or obscured in lateral view (1) (Novas 1989; Carrano et al., 2002).

34. Promaxillary fenestra of maxilla absent (0), or present, clearly visible in lateral view (1), or present and concealed from lateral view by lateral lamina of maxillary antorbital fossa (2) (modified from Holtz, 1994, 1998). (O)

The promaxillary fenestra was hypothesized to be the osseous trace of an anterior expansion of the archosaurian antorbital cavity in some theropod taxa (Witmer, 1997). The fenestra perforates the anteroventral or medial wall of the maxillary antorbital fossa, thereby giving a hypothesized pneumatic diverticulum access to the base of the maxillary dorsal process. The promaxillary fenestra is therefore oriented mostly in a transverse plane (= vertical plane perpendicular to the long axis of the maxilla). The fenestra varies in relative size and degree of development. The space excavated inside the base of the maxillary dorsal process is the promaxillary recess (Wimer, 1997).

The promaxillary fenestra is present in a large number of basal theropods, including most of the taxa included in this study. It is often overlooked or judged absent because its visibility in lateral view depends upon how deeply the maxillary antorbital fossa excavates the maxillary dorsal process, how large and posteriorly extensive the lateral lamina of the maxillary dorsal process is, and the size of the fenestra itself. The quality of preservation of a specimen, and the degree and quality of its preparation can also effect the assessment of this feature's presence. It was also suggested that ontogeny may play role in the degree of pneumatization present in theropod skulls (Witmer, 1997), so it is possible that a very immature specimen may not have a promaxillary fenestra.

The promaxillary fenestra is not present in the type skull of *Eoraptor*, although both maxillae are slightly crushed in this area. It is present in at least three coelophysoid

taxa, *Dilophosaurus*, *Zupaysaurus*, and *"Syntarsus" kayentakatae* (Welles, 1984; Witmer, 1997:fig 31; Tykoski, 1998; Coria and Arcucci, 2003). In all three, the promaxillary fenestra is small and ovoid, opens posterolaterally, and is just barely visible in lateral view (Fig. 22A,B). The fenestra provides passage to a small promaxillary recess in the base of the maxillary dorsal process (Fig. 22C). *Dilophosaurus* may have additional cavities within the dorsal process (TMM 43646-1, UCMP 37303), but it is not clear at this time if they were connected in any way to the promaxillary recess. A promaxillary fenestra was not reported in either *Coelophysis* or *Syntarsus rhodesiensis*, and is considered absent in these taxa.

The promaxillary fenestra was said to be absent in *Ceratosaurus nasicornis* (Witmer, 1997) (based upon the type-USNM 4735), but present in the abelisauroids *Abelisaurus* and *Carnotaurus*. However, Madsen and Welles (2000) illustrate a well-preserved *Ceratosaurus* maxilla with a promaxillary fenestra. The structure was scored as present in the taxon by both Carrano et al. (2002) and Rauhut (2003). A small aperture is also visible in the anteroventral corner of the maxillary antorbital fossa of the abelisauroids *Abelisaurus* and *Carnotaurus*, and a visible promaxillary fenestra is also scored as present in these taxa.

The promaxillary fenestra was scored as present in the abelisauroids *Majungatholus*, *Masiakasaurus*, and *Noasaurus* by Carrano et al. (2002). It is difficult to verify from the published images if there is a promaxillary fenestra in *Majungatholus*, but I tentatively follow Carrano et al. (2002) in coding the feature as present. The description of the maxilla of *Masiakasaurus* stated there were no additional foramina in the maxillary

antorbital fossa, but it was suggested that the anterior invagination of the maxillary antorbital fossa might constitute a feature homologous to the promaxillary fenestra. The structural relationship of the promaxillary fenestra to the rest of the maxillary antorbital fossa was explicitly spelled out by Witmer (1997), and it differs from the invagination cited by Carrano et al. (2002). The medial and lateral laminae of the maxillary dorsal process enclose a space between them in all theropod maxillae that possess distinct laminae. This space is not homologous to the promaxillary fenestra or the promaxillary recess. Witmer (1997) specifically cited *Noasaurus leali* as another taxon that lacks a promaxillary fenestra, and the fenestra is scored as absent in both *Masiakasaurus* and *Noasaurus*.

35. Medial lamina of dorsal process of maxilla smooth and continuous (0), or with deep accessory pneumatic excavation (1) (Carrano et al., 2002).

Ceratosaurus has a deep pneumatic excavation (=excavatio pneumatica of Witmer, 1997) in the medial lamina of the maxillary dorsal process, a feature easily seen in the type and referred material of the taxon. The pneumatic excavation in this taxon differs from the maxillary fenestra of tetanurans in that the excavation is an enclosed pocket that does not open into a maxillary antrum, and does not communicate with any adjacent maxillary accessory cavities. A pneumatic excavation is also present in the medial lamina of the maxillary dorsal process of *Masiakasaurus*.

A shallower and less distinct excavation in the same area of *Allosaurus* was identified as the pneumatic excavation (Witmer, 1997), but it is not as deep or well

defined as the excavations in *Ceratosaurus* and *Masiaksasaurus*. A number of shallow fossae at least as well developed as that in *Allosaurus* were described in the anterior margin of the maxillary antorbital fossa of *Syntarsus rhodesiensis* (Raath, 1977). Similar features are present in at least some specimens of *Coelophysis* (CM 31375, see Witmer, 1997:fig. 14A).

Carrano et al. (2002) scored this feature as present in both *Masiakasaurus* and *Ceratosaurus*, but also in *Afrovenator*, *Eustreptospondylus*, and *Torvosaurus*. The equivalent character was scored as present in *Ceratosaurus*, *Eustreptospondylus,* and *Torvosaurus* by Holtz (1998). The large aperture in this area of "*Poekilopleuron*" *valedunensis* is closed medially, but is identified as a maxillary fenestra similar to *Eustreptospondylus* (Allain, 2002). There is obviously still confusion as to the nature of the theropod maxillary accessory cavities identified and described by Witmer (1997). I confidently score this character present in *Ceratosaurus* and *Masiakasaurus*, but tentatively score it present in *Torvosaurus*, and absent in *Eustreptospondylus* and "*Poekilopleuron*" *valedunensis* (see below).

36. Medial lamina of maxillary antorbital fossa solid (0), or perforated by maxillary fenestra (1) (Gauthier, 1986).

Details of the maxillary fenestra and its associated structures were discussed extensively by Witmer (1997). The only current uncertainty relates to the identification of accessory maxillary cavities in *Eustreptospondylus* and "*Poekilopleuron*" *valedunensis*. The opening is medially closed in both these taxa, leaving the possibility

the structure is the pneumatic excavation of the maxillary dorsal process discussed above. However, medial enclosure of the maxillary fenestra and its antrum is known in other taxa, *Marshosaurus bicentesimus* being cited and illustrated as an example by Witmer (1997:fig. 29C,D). The size, shape, and depth of the aperture in "*Poekilopleuron*" *valedunensis* correspond well with the maxillary fenestra of *Marshosaurus*. Illustrations of the maxilla of *Eustreptospondylus* appear congruent with the morphology of "*Poekilopleuron*" *valedunensis*, and I score the maxillary fenestra present in both taxa.

37. Anteromedial/palatal process of maxilla short, protrudes little beyond maxilla's anterior process (0), or is long, finger-like projection (1), or long, dorsoventrally tall, mediolaterally narrow, and platelike (2). (UO)

The anteromedial process (=palatal process) of the maxilla usually extends anteriorly from the anteromedial surface of the bone. In most theropods the process also slopes slightly anteroventrally. It is not entirely clear what elements the anteromedial process contacted medially, either its conterpart from the other maxilla or the vomer. The ambiguity is a result of the scarcity of articulated, undamaged skulls of basal theropods that preserve these relationships. The process usually extends only slightly beyond the anterior rim of the maxillary anterior process (Fig. 23A).

The anterior process of the maxilla is long and narrow in *Dilophosaurus*, *Coelophysis*, *"Syntarsus" kayentakatae*, and *Syntarsus rhodesiensis* (Figs. 10C, 23B,C). The anterior terminus of the finger-like projection extends far forward, articulating with the fossa on the medial surface of the premaxilla's posteroventral flange. The maxillary

anterior process then lies medial and ventral to the premaxilla's maxillary process in an articulated skull.

38. Medial surface of anteromedial process of maxilla smooth (0), or bears longitudinal ridges (1) (Sereno et al., 1998).

The medial surface of the anteromedial process bears a pair or more of longitudinally oriented grooves and ridges in most theropods. The ridges are clearly present on the anteromedial process of *Dilophosaurus* (Fig. 24A). The grooves and ridges are absent in *Coelophysis*, *"Syntarsus" kayentakatae*, and *Syntarsus rhodesiensis* (Fig. 24B). The distribution of this feature is unknown in other coelophysoids. Clearly there was a loss of some interlocking relationship between elements in these taxa, be it between opposing anteromedial processes or between the process and the vomer. The relationship between the premaxilla, maxilla, and anterior end of the vomer is very poorly understood in these taxa, because of the lack of adequate preservation in known specimens.

39. Nasals are separate (0), or partially fused, either at anterior end or within median crests or prominences (1), or fused over entire length (2) in adults (modified from Sereno, 1999a). (O)

Ceratosaurus is known for the midline nasal crest on the dorsal skull surface, which is derived from median fusion of dorsally projecting nasal laminae. The rest of the median contact between the two nasals is open in this taxon. The nasals of the recently

described ceratosauroid *Rugops primus* are fused anteriorly, but remain separate posteriorly (Sereno et al., 2004). *Rugops* does not bear dorsal crests or eminences on the skull roof, so the partial fusion of the nasals in this taxon appears to be independent of cranial ornamentation. Spinosaurids (e.g., *Baryonyx*, *Irritator*) also exhibit fusion along only a part of the median nasal suture. In these taxa the posterior end of the nasals are dorsally expanded to form a low median crest, which is fused in the vicinity of the crest only. Previous analyses did not account for a condition in which only part of the nasal suture was obliterated by median fusion. Abelisaurids are derived in that the nasal bones co-ossify and fuse along their entire length. This condition independently evolved in some other theropod taxa, including tyrannosaurid tetanurans.

40. Lateral margin of nasal simple (0), or bears low expanded ridge (1), or forms part of parasagittal crest rising from dorsolateral margin of skull (2), or forms all of thin parasagittal crest (3) (modified from Holtz, 1998).

The nasal bones of at least four coelophysoid taxa contribute to structures on the dorsal or dorsolateral skull margins. The lateral margin of the nasals of *Coelophysis* and *Syntarsus rhodesiensis* bear slightly swollen, longitudinal ridges. The nasal may also project laterally over the dorsal edge of the lacrimal and maxilla. The ridges and laterally overhanging nasals are best observed in specimens of *Coelophysis* that are more dorsoventrally flattened, rather than mediolaterally (i.e., AMNH 7223, AMNH 7240, AMNH 7241). The ridges are most pronounced along the anterior and medial parts of the nasal's length, with the lacrimal forming most of the dorsolateral margin of the rostrum

just anterior to the orbit. The nasals on the type skull of *Eoraptor* flare laterally as well,. *Allosaurus* also has nasals that bear low ridges along their lateral margin.

The paired parasagittal crests on the skull of *Dilophosaurus wetherilli* are exceptionally large and distinctive. The original description of these structures (Welles, 1984) did not recognize certain aspects of their anatomy. At the behest of Dr. K. Padian (pers. comm., April, 2003) I refrain from giving a description of the crest morphology in the skull of UCMP 77270, the only specimen that preserves a large percentage of the delicate crests.

The type skull of *"Syntarsus" kayentakatae* (MNA V2623) preserves the remnants of a cranial crest near the left side of the skull's dorsal surface (Fig. 25A) (Rowe, 1989). There were reportedly two crests originally preserved on the specimen, but the crest on the right side was destroyed during preparation before it could be photographed or otherwise documented (Rowe, pers. comm). The crest morphology in this taxon is very simple compared to that of *Dilophosaurus*, being little more than a low laminar structure. There does not appear to be any contribution from the lacrimal in the formation of the crest, unlike the condition in *Dilophosaurus*. The crest rises from a plane inset medially from the lateral margin of the skull roof. The crest is not a dorsal extension of the lateral surface of the rostrum as it is in *Dilophosaurus*. X-ray CT imagery shows the crest is canted at a dorsolateral angle above the dorsal skull surface (Fig. 25B, C), and does not arc dorsolaterally as in *Dilophosaurus*.

Zupaysaurus rougieri also has paired dorsal skull crests that bear remarkable similarity to those present in *"Syntarsus" kayentakatae* (Arcucci and Coria, 2003). The

delicate crests are also comprised entirely of the nasals, and run for approximately the same relative distance along the skull roof. *Zupaysaurus* was described as an early tetanuran theropod (Arcucci and Coria, 2003), but my pre-analyses show it is a coelophysoid theropod. The presence of two taxa with thin crests formed entirely by the nasal bones is a potential phylogenetic feature. An additional character state recognizes the distinction between nasolacrimal and nasal crests.

Because of the mediolateral crushing of the rostrum in the specimens of *"Syntarsus" kayentakatae* and *Zupaysaurus*, and the apparent telescoping of the nasals and other rostrum elements, it is possible that the structures interpreted as crests in these skulls might actually be the lateral margins of the nasals. The edge of a flat bone is visible through the left internal antorbital fenestra just medial to the left maxilla and lacrimal in MNA V2623. It appears to lie in the same plane as the crest and is in the correct position to be a ventrolaterally displaced left nasal. X-ray CT imagery of this region is not clear enough to overturn the hypothesis that the structure in question is a dorsal skull crest (Fig. 25B, C). If there were not data regarding the presence of a second, right-side crest in the MNA V2623 specimen at the time of its discovery, it would be more parsimonious to identify the dorsal skull crest of *"Syntarsus" kayentakatae* as the lateral part of the left nasal bone.

41. Dorsal surfaces of nasals relatively smooth (0), or rugose, with heavy pitting and sculpturing (1) (Holtz, 1998).

42. Lateral or posterolateral surface of nasal solid (0), or perforated by pneumatic foramen/foramina (1) (Forster, 1999).

43. Lateral surface of anterior end of nasal along margin of external naris relatively flat (0), or with concave fossa (1), or with laterally convex hood covering posterior part of external naris (2) (Tykoski, 1998; Carrano et al., 2002). (UO)

This lateral surface of the nasal along the external naris margin is relatively flat in *Lesothosaurus*, *Eoraptor*, and *Herrerasaurus* (Fig. 26A). The nasal is laterally concave in *Plateosaurus* and other basal sauropodomorphs. The anterior end of the nasal bears a lateral concavity where it borders the external naris of most theropod taxa (Fig. 26B). The most notable exceptions in this analysis are *Ceratosaurus* and some abelisaurid taxa, in which the nasal is strongly convex outward over the osterior part of the external naris (Gilmore, 1920; Bonaparte et al., 1990; Sampson et al., 1998). This feature is seen clearly in *Ceratosaurus* (see Madsen and Welles, 2000:pl. 3A-D), *Carnotaurus*, and *Majungatholus*. This morphology of the nasals is especially developed in *Carnotaurus*. The nasals form such overhanging, hood-like structures in this taxon that the aperture of the external naris is barely visible in lateral view.

44. Nasal excluded from (0), or contributes to border of (1) antorbital cavity (Holtz, 1998).

45. Frontals anteroposteriorly short and approximately rectangular (0), or elongated and triangular (1) in dorsal view (Holtz, 1994).

46. Frontals remain separate (0), or indistinguishably fuse to each other (1) in adults (Holtz, 1998).

47. Frontals relatively flat (0), or contribute to dorsal skull roof prominences (i.e. horns, knobs, bosses) (1), or bear large, laterally positioned supraorbital horns (2) (Coria et al., 2002). (O)

The skulls of the abelisaurids *Aucasaurus*, *Carnotaurus*, and *Majungatholus* each bear conspicuous dorsal enlargements of the frontal bones, and the presence of such structures is treated here as a discrete character. As with the modifications of the nasals in coelophysoids and other taxa, there are two distinct pathways represented in the pattern of frontal enlargement in these taxa. The fused frontal bones of *Majungatholus* bear a single, dome-shaped horn on the dorsal skull surface (Fig. 15A). It was the discovery of an isolated frontal dome that led workers to coin the name *Majungatholus atopus*, and refer the taxon to Pachycephalosauria (Sues and Taquet, 1979). The frontals form the posterior part of a median dorsal skull prominence in the Indian abelisaurid *Rajasaurus* (Wilson, et al., 2003), but that taxon is not included in this analysis. The unified frontal bones of *Aucasaurus* and *Carnotaurus* each bear very robust, blunt, paired horns that project dorsolaterally from a point just anterodorsal to the orbits (Fig. 15B).

48. Frontals and parietals remain separate (0), or fuse (1) in adults (Holtz, 1998; Forster, 1999; Sereno, 1999a).

49. Frontal-parietal contact area relatively flat (0), or with median fossa in saddle-shaped depression (1) (Sampson et al., 1998).

50. Dorsal surface of parietal relatively flat (0), or with transversely thickened sagittal crest between supratemporal fenestrae (1) (Novas, 1989; Holtz, 1998).

51. Parietal nuchal crest relatively small, thin (0), or greatly enlarged and elevated (1) (Forster, 1999; Sereno, 1999a).

52. Lacrimal blocky or triangular (0), or an inverted L-shape (1) in lateral view (modified from Rauhut, 2003).

53. Lacrimal dorsoventrally shorter than orbit and fails to reach level of orbit's ventral rim (0), or as tall or subequal to height of orbit with ventral end that reach level of orbit's ventral rim (1) (modified from Rauhut, 2003).

This and the following character were combined and treated as a single feature by Rauhut (2003). The two states may not be entirely correlated though. The lacrimal of some basal sauropodomorphs is dorsoventrally tall, but does not resemble an 'inverted L-

shape' in lateral view. This indicates there may be some variability in these states at the base of Saurischia. I separate these potentially independent characters.

54. Anterior ramus of lacrimal dorsoventral height approximately equal (0), or much narrower (1) than anteroposterior width of ventral ramus of lacrimal (Sereno et al., 1996).

The reference points from which the relative dorsoventral width of the lacrimal anterior ramus were measured are shown in Figure 27A. The reference points for measurements coded in following two characters are also shown in Figure 27A. The reduction in the dorsoventral thickness of the lacrimal's anterior process (=anterior ramus) in *Torvosaurus*, *Afrovenator*, and spinosaurids was noted by Sereno et al. (1996) (Fig. 27B). The condition is also present in several taxa other taxa, including the abelisaurids *Carnotaurus* and *Majungatholus*, and "*Poekilopleuron*" *valedunensis* (Fig. 27C). The narrowing of the lacrimal's anterior process is just one component in the extreme reduction of the process in abelisaurid taxa. Other variables reflecting alterations to lacrimal morphology are addressed below.

55. Ratio of lacrimal anterior ramus length versus ventral ramus length 0.65≤1.00 (0), or < 0.65 (1), or >1.00 (2) (Sereno et al., 1996; Tykoski, 1998). (UO)

The length of the anterior process of the lacrimal is less than the length of the ventral ramus in most theropods. It measures between 65% and 100% the length of the ventral process in *Plateosaurus*, *Herrerasaurus*, *Eoraptor*, *Dilophosaurus*, *Ceratosaurus*,

Torvosaurus, *Irritator*, "*Poekilopleuron*" *valedunensis*, and *Allosaurus* (Fig. 27A, B). The measurement of the length of the anterior ramus is taken from the posterior-most rim of the lacrimal's dorsal end to the anterior most tip of the lacrimal possible. This includes as much of the element that may be medial to the dorsal process of the maxilla as can be seen in an articulated skull, not just the laterally exposed maxilla-lacrimal contact above the internal antorbital fenestra.

The anterior process of the lacrimal is short (<65%) relative to the ventral ramus of the bone in *Lesothosaurus*, the abelisaurids *Aucasaurus*, *Carnotaurus*, and *Majungatholus*, and the spinosaurids *Baryonyx*, and *Suchomimus* (Fig. 27C). The reduction of this anterior component of the lacrimal is especially strong in the abelisaurid taxa, in which the anterior ramus is effectively absent. This feature, coupled with the short dorsal process of the maxilla in abelisaurids, results in the lack of contact between the anterior ramus of the lacrimal and the dorsal process of the maxilla (Fig. 15).

The length of the anterior ramus of the lacrimal exceeds the dorosventral height of the ventral ramus in some coelophyoids (Fig. 27D). These include *Coelophysis*, *"Syntarsus" kayentakatae*, and *Syntarsus rhodesiensis*. The lack of adequate cranial material for other coelophysoids more derived than *Dilophosaurus* makes it impossible to ascertain the exact node diagnosed by this apomorphy. The condition is also present in *Zupaysaurus* (Arcucci and Coria, 2003).

56. Lacrimal does not contact postorbital (0), or bears posterior process that contacts postorbital, excluding frontal from rim of orbit: absent (1) (Sampson et al., 1998).

57. Lacrimal antorbital fossa without (0), or with (1) deep pneumatic recesses in posterodorsal corner of lacrimal (Novas, 1989; Holtz, 1998).

58. Lateral lamina of lacrimal ventral ramus linear and remains posterior to medial lamina (0), or sinuous and protrudes anteriorly beyond medial lamina (1). See Figure 27B and 27D.

59. Lacrimal antorbital fossa small or nonexistent (0), or large, excavates laterally open triangular fossa on lacrimal ventral ramus (1).

The ventral ramus of the lacrimal in *Herrerasaurus*, *Plateosaurus*, and most other basal sauropodomorphs bears a small lacrimal antorbital fossa. The fossa usually has irregular, curving margins and a weak posterior rim (Fig. 28A, B). The lacrimal antorbital fossa is large and approximately triangular in *Eoraptor* and all the other theropods in this study, with the exception of the abelisaurids (Fig. 28C, D). The fossa usually has a well-defined, raised posterior margin that delineates the posteroventral edge of the antorbital cavity.

This feature is not well preserved in the neotype of *Coelophysis bauri* (AMNH 7224). The ventral ramus of the lacrimal in that specimen is extraordinarily narrow and featureless, to the point that even the medial and lateral laminae of the lacrimal (sensu Witmer, 1997) are not easily differentiated. A number of other *Coelophysis* specimens exhibit a distinct triangular fossa on the ventral ramus of the lacrimal (e.g., AMNH 7241,

YPM 41196, MNA 3315, MCZ 4327), suggesting the lack of the feature in the neotype may be a preservational artifact.

The morphology of the lacrimal of *Syntarsus rhodesiensis* was described and illustrated based on multiple but disarticulated specimens (Raath, 1977). Comparison of the description of the isolated lacrimals of *S. rhodesiensis* to articulated lacrimals of *"Syntarsus" kayentakatae* and *Coelophysis* reveals that the descriptions of the lateral and medial surfaces of the element were reversed for *S. rhodesiensis*. In other words, the description of the medial surface of the lacrimal provided by Raath (1977) is a match with the lateral surface of the lacrimal in articulated skulls of *Coelophysis* and *"Syntarsus" kayentakatae*. The misidentification of the medial and lateral surfaces of the lacrimal probably contributed to the unusual relationship of the lacrimal, jugal, and maxilla in reconstructions of the skull in *S. rhodesiensis* (Raath, 1977).

60. Lacrimal not dorsally enlarged (0), or with distinct "horn" (=posterodorsal boss or blade) (1) (Rauhut, 2003).

61. Lacrimal ventral process with relatively linear orbital margin (0), or with suborbital process/posterior convexity (1) (Sampson et al., 1998).

62. Postorbital long-axis oriented nearly vertical (0), or anteroventral-posterodorsal (1) (Novas, 1989, Carrano et al., 2002).

63. Ventral (=jugal) process of postorbital nearly linear or slightly curved (0), or with distinct suborbital process (1) (Gauthier, 1986, Holtz, 1998).

64. Ventral (=jugal) process of postorbital transversely narrow with triangular cross-section (0), or broad with U-shaped cross-section (1) (Sereno et al., 1994).

65. Postorbital with stepped-down ventrolateral fossa: absent (0), or present (1) (Sampson et al., 1998, Carrano et al., 2002).

66. Anterior process of postorbital dorsally higher than posterior process (0), or at about same level as posterior process, resulting in T-shaped postorbital (1) (Currie, 1995; Holtz, 1998).

67. Jugal-maxilla overlap length <50% (0), or ≥50% (1) total jugal length (Sampson et al., 1998).

This character is present in the abelisaurids *Carnotaurus* and *Majungatholus*, as well as in *Ceratosaurus*. It is also present in the purported basal theropod *Eoraptor*. This character was scored as present in *Dilophosaurus* by Carrano et al. (2002). Examination of the type specimen (UCMP 37302) shows this is not the case (Fig 20A, B). The jugal is missing the posterior tip of the ventral posterior prong in UCMP 37302. The amount of maxilla-jugal overlap in the specimen does not equal even 50% of the remaining part of

the jugal, and would constitute a still smaller percentage of the overall length of a complete jugal. I code this feature as absent in *Dilophosaurus*.

68. Anterior process of jugal abuts lacrimal (0), or bears dorsal flange that laterally overlaps ventral process of lacrimal (1) (modified from Sereno et. al., 1994; Carrano et al., 2002).

69. Jugal contacts internal antorbital fenestra (0), or does not contact internal antorbital fenestra, participates in external antorbital fenestra (1), or no participation in external antorbital fenestra (2) (Holtz, 1998; Carrano et al., 2002). (UO)

Among the outgroups in this study the jugal enters the internal antorbital fenestra in *Herrerasaurus*, and *Lesothosaurus* (Fig. 28C). The jugal does not reach the internal antorbital fenestra in *Plateosaurus* (SMNS 13200) (Galton, 1984b; contra Rauhut, 2003), but it does reach the margin of the external antorbital fenestra. Among the ingroup theropods the jugal contributes to the rim of the internal antorbital fenestra in *Dilophosaurus*, *Zupaysaurus*, *Carnotaurus*, and *Majungatholus*. The jugal participates in the external antorbital fenestra, but does not reach the internal antorbital fenestra in "*Syntarsus" kayentakatae*, *Irritator*, and *Allosaurus*. Jugal participation in the external antorbital fenestra was scored as absent by Carrano et al. (2002) for *Coelophysis* and *Syntarsus*, even though reconstructions of the skull of *Coelophysis* showed the jugal within the antorbital fossa and even contacting the rim of the internal antorbital fenestra (Colbert, 1989). Photographs published with the cranial reconstructions did not provide

enough detail or clarity to support or refute either claim. The cranial reconstructions used by Colbert (1989) closely approximate the skull of AMNH 7224. This specimen (the neotype of *C. bauri*) bears several preservational artifacts. I follow Carrano et al. (2002) and scoring the jugal not reaching the external antorbital fenestra in *Coelophysis* and *Syntarsus rhodesiensis*. The anterior process of the jugal is too incomplete or poorly preserved in the remaining ingroup taxa to evalaute this character.

The anterior tip of the jugal in *"Syntarsus" kayentakatae* is mediolaterally flattened and bears three small processes (Fig. 28D). The dorsal two of these processes lap over the ventral part of the lacrimal, while the most ventral process tapers to a blunt anterior projection. The ventral process appears to have a weak interlocking joint with a notch in the posterior end of the maxilla, an unusual arrangement in theropods. This morphology does not clearly fit the character states listed by Rauhut (2003) in his character number 23, which lists either 'tapered', 'bluntly squared', or 'expanded' as possible states. A jugal of *Syntarsus rhodesiensis* (QG278) was scored as 'bluntly squared anteriorly' in that analysis. However, the same jugal cited by Rauhut (2003) was illustrated by Raath (1977:fig. 4u) with a weak anterior taper, but not the abruptly squared-off end illustrated by Rauhut. The jugal in *Syntarsus rhodesiensis* bears no indication of the weakly expanded anterior process of the jugal in *"Syntarsus" kayentakatae*. A very small portion of the antorbital fossa may be expressed on the anterior edge of the jugal in *"Syntarsus" kayentakatae*, including the ventral and middle of the three anterior processes (Fig 28D). I consider the antorbital fossa to be expressed

on the jugal in *"Syntarsus" kayentakatae* until additional articulated material proves otherwise.

The jugal was scored as not participating in the antorbital fossa of *Carnotaurus* and *Majuntholus* by Carrano et al. (2002). The antorbital fossa is strongly reduced in these taxa, especially in its ventral and posterior expression. Yet the jugal actually reaches the border of the internal antorbital fenestra in these taxa. I can only guess that the authors of the analysis assumed that the reduction or loss of the antorbital fossa in this area removes the possibility of the jugal contributing to the fossa. If there is the slightest bit of depression or inset along the ventral and posteroventral rim of the internal antorbital fenestra in these forms, it constitutes an antorbital fossa. The jugal still traverses the area where the rostrum is excavated by the antorbital fossa. The jugal did not undergo an evolutionary transformation in these taxa, but rather the antorbital cavity did. This transformation was already addressed as a separate character above. Jugal participation in the internal antorbital fenestra is present in these two taxa.

70. Posterior process of jugal undivided (0), or divided, ventral prong subequal or much shorter than dorsal prong (1), or divided with ventral prong much longer than dorsal prong (2) (modified from Gauthier, 1986; Sereno and Novas, 1993; Sereno et al., 1993; Holtz, 1998). (O)

The posterior process (=quadratojugal process) of the jugal is a tapered, undivided projection in *Plateosaurus* (Galton, 1984b) (Fig. 29A). It is divided into dorsal and ventral prongs for articulation with the quadratojugal in *Herrerasaurus*, *Eoraptor*, and

other theropods. In *Herrerasaurus* the two prongs are roughly equivalent in length, projecting about the same distance posteriorly. In *Eoraptor* the dorsal prong is about twice length of the ventral prong (Fig. 29B; pers. obs. PVSJ 512). The two prongs of the posterior process of the jugal are also almost equal in length in the abelisaurids *Carnotaurus* and *Majungatholus* (Bonaparte et al., 1990; Sampson et al., 1998). The posterior process of the jugal in most other basal theropods has a ventral prong that is much longer than the dorsal prong.

The posterior process of the jugal was described as rod-like and not divided in *"Syntarsus" kayentakatae* and *Coelophysis* by Tykoski (1998). The quality of preservation of many *Coelophysis* skulls renders this judgement untenable. Closer examination of the left jugal in MNA V2623 (*"Syntarsus" kayentakatae*) reveals the process is divided as in other theropods. There is a small dorsal prong that is nearly concealed by the slightly displaced, overlapping anterior process of the quadratojugal (Fig. 29C). The assessment that a double-pronged posterior process of the jugal was absent in "*Syntarsus*" *kayentakatae* by Tykoski (1998) was incorrect, and is revised here.

71. Lateral surface of jugal flat (0), or with low rounded ridge that traverses anterior and posterior processes (1) (Sereno and Novas,1993; Tykoski, 1998).

72. Ventral process of squamosal narrow (0), or broad and/or expanded (1) (Rauhut, 2003).

73. Quadratojugal and squamosal contact small (0), or broad (1), or absent (2) (modified from Holtz, 1998; Rauhut 2000, 2003). (UO)

In most theropods, and most archosaurs for that matter, there is at least some degree of contact between the dorsal ramus of the quadratojugal and the ventral process of the squamosal. Abelisaurids are the exception to this pattern within Theropoda. There is uncertainty about the coding of this character among some other basal theropods. For example, Rauhut (2003) scored no squamosal/quadratojugal contact in *Dilophosaurus* and *Syntarsus*, the latter based upon the initial description of the material (Rowe, 1989).

The type skull of *Dilophosaurus* (UCMP 37302) is badly crushed, and the dorsal ramus of the quadratojugal may not be complete (Fig. 20). If any of the squamosal is preserved it is likely it is displaced, and Welles (1984) was probably correct when he stated that the ventral extremity of the squamosal's ventral process is missing in the specimen. Given these observations I score this character as missing data for *Dilophosaurus*.

The left squamosal and quadratojugal in type skull of *"Syntarsus" kayentakatae* are articulated, but both are dorsoventrally crushed and broken (Fig 30A). This prevents an accurate determination of this character in the articulated material. The disarticulated right squamosal and quadratojugal (still articulated with the right quadrate) are well preserved (Fig. 30B). Measurements of the squamosal's ventral process and the distance between the dorsal quadrate head and the dorsal margin of the quadratojugal suggest the quadratojugal and squamosal probably did contact when they were articulated. The tips

of both processes taper toward one another, so it is likely contact between the two was limited.

74. Quadratojugal and quadrate remain separate (0), or fuse (1) in adults (Holtz, 1994, 1998).

The quadrate and quadratojugal are indistinguishably fused to one another in adult abelisaurid specimens, as well as in *Ceratosaurus*. Fusion between these two elements was also reported in *Zupaysaurus* (Coria and Arcucci, 2003). In other theropods these two elements are firmly sutured to one another, but do not co-ossify. Quadratojugal-quadrate fusion was scored as absent in *Dilophosaurus* by Carrano et al. (2002), and in all likelihood this was the condition present. Unfortunately, the only adult specimen of this taxon is UCMP 77270, and it does not preserve either of these bones. I score this character as missing data for *Dilophosaurus*.

75. Quadrate short or moderately tall and dorsoventrally oriented (0), or tall and posteroventrally angled so ventral condyle is posterior to dorsal condyle and paraoccipital processes (1) (modified from Rauhut, 2003).

76. Quadrate foramen small and surrounded mostly by quadrate (0), or absent (1), or large and surrounded by near equal shares of quadrate and quadratojugal (2) (modified from Novas, 1989; Holtz, 1998; Carrano et al., 2002; Rauhut, 2003). (UO)

The relative size, position, and even presence of the quadrate foramen are variable among Theropoda, but some patterns can be assessed for phylogenetic purposes. Recent phylogenetic analyses were contradictory in their assessment of the feature. For example, the quadrate foramen was scored as 'reduced or absent' by Holtz (1998), as 'large/at edge [of quadrate]' by Carrano et al. (2002), and as missing data by Rauhut (2003) for *Coelophysis* and *Syntarsus*. There was no consensus as to what constitutes a large or small quadrate foramen, and what should be considered marginal versus enclosed by the quadrate.

The following criteria are followed when evaluating the relative position and size of the quadrate foramen. A quadrate foramen is considered on the margin of the quadrate if the quadrate and quadratojugal contribute almost equal amounts to the borders of the foramen (Fig 31A). The foramen is treated as enclosed or encircled by the quadrate if the bone comprises an obvious majority of the foramen's rim (Fig. 31B, C). This can be accomplished either by shifting the foramen medially into the body of the quadrate dorsal ramus, or by the presence of thin spurs of the quadrate that intervene between the quadratojugal and the rim of the foramen. Assessing the relative size of the foramen is more subjective and problematic. The quadrate foramen is 'small' if its largest axis measures 10% or less the dorsoventral height of the quadrate dorsal ramus as measured from the lateral articular condyle to the dorsal squamosal condyle (Fig. 31B, C). The foramen is scored as 'large' if its longest axis is greater than 10% the dorsoventral height of the quadrate dorsal ramus (Fig. 31A).

The quadrate foramen was scored as a distinct opening between the quadrate and quadratojugal in Ornithischia by Rauhut (2003). This condition is found in many derived ornithischians, but the foramen was restored as small and nearly encircled by the quadrate in the basal ornithischian *Lesothosaurus* (Sereno, 1991:fig. 3A). The quadrate foramen is also small and encircled in *Plateosaurus* and other basal sauropodomorphs, *Herrerasaurus*, and *Eoraptor*. Among the tetanurans in this study *Allosaurus* and *Ornitholestes* also share this feature. The same condition is present in the coelophysoids *Dilophosaurus* and *Liliensternus*. Poor preservation and insufficient description renders this character uncertain in *Coelophysis* at this time. The quadrate foramen was described as being "near the edge where it articulates with the quadratojugal" in *Syntarsus rhodesiensis* (Raath, 1977:39), yet illustrations of these elements seem to show a small foramen present on the quadrate-quadratojugal border itself (Raath, 1977:figs. 3d, 4j). I treat the quadrate foramen as small in *Syntarsus rhodesiensis*, but leave characters regarding the position of the foramen coded as missing data.

The quadrate foramen in the type skull (MNA V2623) of *"Syntarsus" kayentakatae* is visible only on the right side. The foramen is small (Fig 31C), much smaller in relative proportions than that in the other coelophysoids discussed here. Post-mortem forces rotated the right quadratojugal posterolaterally with respect to the dorsal ramus of the right quadrate. This caused extensive microfracturing along the quadrate-quadratojugal suture. It appears that the quadrate foramen is largely encircled by the quadrate, although this assessment is tentative at this time.

The quadrate and quadratojugal are not preserved in known specimens of *Marasuchus*, so the morphology present in this and other dinosauriforms is unknown at this time. The presence of a small, partly encircled quadrate foramen in *Lesothosaurus*, *Plateosaurus*, *Herrerasaurus*, *Eoraptor*, several coelophysoids, and some tetanurans suggests the most parsimonious conclusion is that the condition is plesiomorphic for Dinosauria. It is therefore uninformative to treat an enclosed quadrate foramen as a derived character state (contra Holtz [1998], Carrano et al. [2002], and Rauhut [2003]).

The quadrate foramen is not present in *Ceratosaurus*, *Carnotaurus*, and *Majungatholus*. The foramen was scored as lost in *Noasaurusi* by Carrano et al. (2002). It is also apparently absent in the tetanuran *Torvosaurus*, and Carrano et al. (2002) scored the foramen lost in *Eustreptospondylus*. The character was left as missing data for *Eustreptospondylus* by Holtz (1998), but Rauhut (2003) scored the foramen present as a distinct opening between the quadrate and quadratojugal for the same taxon. I was unable to find satisfactory descriptions or illustrations of the relevant material to confidently score the quadrate foramen state in this taxon. This character is coded as missing data for *Eustreptospondylus* in this analysis.

The quadrate foramen is large in a number of tetanuran taxa. It may also be positioned almost directly along the quadrate-quadratojugal border, with nearly equal contributions to its rim by the quadrate and quadratojugal. This morphology is especially prevalent among groups of coelurosaurian theropods. It is also present in the more basal tetanuran *Baryonyx* (Fig. 31A) and probably also *Suchomimus*.

77. Supratemporal fossae widely separated by parietals (0), or in contact posteriorly but separated anteriorly by triangular plate of parietals (1), or confluent so parietals reduced to a sagittal crest (2) (modified from Rauhut, 2003). (UO)

78. Basisphenoid lateral surface not excavated by fossa (0), or excavated by anterior tympanic recess (1) (Rauhut, 2003).

79. Basisphenoidal recess very shallow, poorly developed, or absent (0), or deep and well developed (1) (Rauhut, 2003).

80. Transverse intertuberal lamina of basisphenoid a simple wall (0), or bears small median spur that projects anteriorly along roof of basisphenoidal recess (1).

This feature is present in both *Syntarsus rhodesiensis* and *"S." kayentakatae* (Raath, 1977; Tykoski, 1998). There is no such incipient division of the roof of the basisphenoidal recess in *Dilophosaurus* (UCMP 37302). Few specimens of *Coelophysis* have a well-preserved braincase, and even fewer are oriented to give an adequate view of the basisphenoidal recess. A reconstruction of the ventral view of the braincase was given by Colbert (1989), but it was not very informative. The character is scored as missing data in *Coelophysis*.

81. Cranial nerves X and XI exit skull laterally through metotic (=jugular) fissure (0), or through foramen/foramina on posterior skull surface lateral to occipital condyle and foramen for cranial nerve XII (1) (Rauhut, 2003).

82. Ventral edge of proximal end of paroccipital process is dorsal to (0), or at same level or ventral to (1) horizontal plane through middle of occipital condyle (modified from Rauhut, 2003).

83. Interorbital braincase elements (i.e., interorbital septum or mesethmoid, orbitosphenoid, sphenethmoid) do not ossify (0), or ossify (1) by adulthood (Novas, 1997; Carrano et al., 2002).

84. Ectopterygoid flange of pterygoid flat (0), or marked by fossa (1) (Gauthier, 1986).

85. Ectopterygoid ventral surface flat (0), or with deep fossa (1), or with fossa and deep groove excavated into body of element from medial side (2) (modified from Rauhut, 2003). (UO)

86. Dorsal edge of anterior tip of dentary continuous with mid-dentary (0), or is raised conspicuously relative to middle and posterior parts of dentary (1) (Sereno, 1999a).

This feature is pronounced in specimens of *Dilophosaurus* (UCMP 37303, 77270) and *Liliensternus* (Huene, 1934:pl. 13; figs. 10, 13), but it is variably expressed in the

large sample of *Coelophysis* from the Ghost Ranch locality. Some specimens show an obvious dorsal elevation of the alveolar margin at the tip of the lower jaw (AMNH 7224, 7241), while others show only a little dorsal expansion of the dentary (AMNH 7240, YPM41196) (Figs. 32A, B). The same is true of specimens of *Syntarsus rhodesiensis*. The anterior dentary is raised in *"Syntarsus" kayentakatae* (Fig. 32C). Even greater dorsal enlargement of the anterior dentary is present in *Baryonyx* and *Suchomimus*.

87. Dentary tooth count ≤18 (0), or >18 (1) (Carrano et al., 2002).

Most theropods have fewer than 18 teeth in the dentary. Only *Liliensternus* (>20 dentary teeth), *Coelophysis* (27 dentary teeth), *Syntarsus rhodesiensis* (25 dentary teeth), *Baryonyx* (32 dentary teeth), and *Suchomimus* (32 dentary teeth) unequivocally possess the derived state among those taxa in the present study. CT scans of the skull of *"Syntarsus" kayentakatae* (MNA V2623) show only 16 alveoli in each dentary. It is possible that a very small tooth or alveolus may be present in the most distal position of the tooth row, but this would still tally only 17 dentary teeth in this taxon. In this regard *"Syntarsus" kayentakatae* more closely resembles *Dilophosaurus* (17 dentary teeth) and *Zupaysaurus* (15 dentary teeth) (Welles, 1984; Coria and Arcucci, 2003).

88. Posterodorsal end of dentary without (0), or with (1) socket for surangular prong (Carrano et al., 2002).

89. Posteroventral process of dentary extends further posteriorly than posterodorsal process (0), or subequal in length to posterodorsal process (1) (Sereno, 1999a).

The posterior end of the dentary of most basal theropods is divided into two processes, one ventral to the external mandibular fenestra, and the other dorsal to the fenestra. The dorsal process usually does not extend as far posteriorly as the ventral process. In fact, it may be virtually non-existent and the margin of the dentary slopes posteroventrally from the alveolar border to the rim of the external mandibular fenestra (Fig. 33A). The dorsal and ventral processes of the dentary are subequal in length in *Carnotaurus*, *Majungatholus*, and *Masiakasaurus* (Fig. 33B). The posterior processes of the dentary are also subequal in *"Syntarsus" kayentakatae* (Fig. 33C). The posterior margin of the dentary is not adequately preserved in specimens of *Syntarsus rhodesiensis* to evaluate this character, and known illustrations and reconstructions of the dentary of *Coelophysis* are unclear with regard to this feature. This character is scored as missing data for the latter two taxa.

90. External mandibular fenestra small or moderate in size (0), or very large (1) (Gauthier, 1986; Sampson et al.,1998).

91. Splenial without (0), or with (1) foramen (either closed or ventrally open) near anteroventral margin (Rauhut, 2003).

A foramen near the anteroventral margin of the splenial was cited by Rauhut (2003) as a character variably present within Saurischia. I differ from the scoring of this

feature by Rauhut (2003) for two taxa he left coded as missing data for the character in that analysis. *Herrerasaurus* is known from at least one complete skull (PVSJ 407) which was well figured and thoroughly described (Sereno and Novas, 1993). It was acknowledged that most of the known mandibles of *Herrerasaurus* were closely appressed, obscuring their medial surfaces. The splenial was individually described with no mention of a foramen penetrating its surface, even though pathologies referred to tooth marks were noted in detailed illustration of the element (Sereno and Novas, 1993:figs. 1B, E, F). A cast of this skull in the collections of the Texas Memorial Museum Vertebrate Paleontology Laboratory (TMM 43451-1) verified the illustrations of the specimen in this regard. It is possible that a foramen is located more dorsally in the splenial than what is visible in this specimen. However, the foramen in the splenial of the sauropodomorph *Plateosaurus*, and also in the coelophysoid *"Syntarsus" kayentakatae* is very near the ventral margin of the bone, and is plainly visible. I therefore score this character as absent in *Herrerasaurus* until such time as shown otherwise.

As alluded to above, the splenial in the type skull of *"Syntarsus" kayentakatae* also bears a foramen near its anteroventral margin (Fig. 34). It is visible in left lateral view of the skull. The splenial foramen in this specimen provides the only hard evidence for its presence in coelophysoids as a clade. Known specimens of *Coelophysis* and *Dilophosaurus* are too poorly preserved or prepared at this time to unambiguously state the condition in these taxa.

92. Splenial posterior margin forked (0), or straight, not forked (1) (Rauhut, 2003).

This character was left unscored by Rauhut (2003) in the compound OTU "Baryonichidae" used in that study. A detailed illustration of the splenial of *Baryonyx walkeri* was given by Charig and Milner (1997). A small portion of the dorsoposterior apex of the bone is poorly preserved, but it appears that the splenial has a tapered posterior end that is not forked. The derived state is present in *Baryonyx*.

93. Angular stops short of posterior end of mandible (0), or reaches posterior end of mandible, blocking surangular from ventral margin of jaw in lateral view (1).

94. Retroarticular process of mandible about same mediolateral width (0), or much broader (1) than mandible anterior to jaw joint (Rauhut, 2003).

95. Serrations on mesial-most premaxillary teeth of 'normal' size and number (0), or are very small and few in number, or wholly lacking (1) (Rowe, 1989; Rowe and Gauthier, 1990).

The premaxillary teeth of most basal theropods bear serrations along meso-distal carinae, much the same as are present on the maxillary teeth. The mesial-most premaxillary teeth of at least some coelophysoids either lack serrations, or have serrations that are very reduced in size and number. The premaxillary teeth of *Syntarsus rhodesiensis* were described as lacking serrations, and there was no mention of carinae on the teeth (Raath, 1977). The mesial three premaxillary teeth lack carinae and serrations, and the fourth bears only mesodistal carinae in *Coelophysis* (Colbert, 1989). The first

two premaxillary teeth of *"Syntarsus" kayentakatae* lack serrations and carinae (Fig. 35A, B). It is unclear at this time if carinae or serrations are present on the distal premaxillary teeth of this taxon.

The first premaxillary tooth is not present in preserved specimens of *Dilophosaurus*, but the second tooth reportedly bears fine mesial and distal serrations. The third tooth lacks even a carina on its mesial edge, but is serrated along its distal margin. The fourth premaxillary tooth is poorly preserved, but apparently lacks serrations on both margins. The disjunct distribution of serrations and carinae on the premaxillary teeth, and the very fine nature of the serrations themselves leads me to score this character as present in *Dilophosaurus*.

96. Mesial premaxillary teeth cross-section labiolingually flattened (0), or subcircular (1) or asymmetrical, "D"-shaped (2) (Rowe, 1989). (UO)

The premaxillary teeth of most theropods, and most archosaurs that possess premaxillary teeth, are labiolingually flattened, with minor variations in the convexity of the crown. Some coelophysoids differ from the usual pattern in that at least the mesial premaxillary teeth are subcircular to circular in cross-section. Such a condition is present in *Coelophysis*, *Syntarsus rhodesiensis*, and *"Syntarsus" kayentakatae* (Fig. 35A). There may be variation between taxa in the degree of roundness of the distal premaxillary teeth. The fourth premaxillary tooth in *Coelophysis* was described as labiolingually flattened relative to the more mesial three teeth (Colbert, 1989). No distinction was made in shape of the premaxillary teeth of *Syntarsus rhodesiensis* (Raath, 1977). It appears that the

distal-most premaxillary tooth is slightly more compressed than the mesial teeth in *"Syntarsus" kayentakatae*. It is not clear if the next-to-last tooth is also more labiolingually compressed than the more mesial teeth.

The mesial two alveoli in the left premaxilla of *Dilophosaurus* (UCMP 37303) are circular in ventral view, but this does not necessarily indicate the teeth positioned there were also circular in cross-section. The right premaxilla of UCMP 37303 was not located at the time I examined the UCMP *Dilophosaurus* material, so the shape of the second premaxillary tooth in that specimen is not known. The left third and fourth premaxillary teeth have thick, strongly convex cross-sections, especially the third. Most workers would not consider them subcircular in section. The character is scored as missing data for *Dilophosaurus*.

97. Long axis of mesial premaxillary teeth recurved (0), or nearly straight (1) (Rowe, 1989).

The long axes of the mesial premaxillary teeth of most basal theropods have a obvious distalward curve as the axes pass from the tooth base towards the tip of the tooth crown. Some coelophysoids have a derived condition in which the axes of the mesial teeth are very weakly recurved, or straight. This apomorphy is visible in the mesial-most premaxillary tooth of *"Syntarsus" kayentakatae* (Fig. 35A). The more distal premaxillary teeth exhibit successively greater degrees of axial recurvature, with the last premaxillary tooth being nearly as recurved as the maxillary teeth. Similar teeth are present in specimens of *Coelophysis* (AMNH 7240, MCZ 4327) and *Syntarsus rhodesiensis*.

98. Maxillary interdental plates remain separate (0), or fuse to each other (1) (Rauhut, 1995; Holtz, 1998).

Fused interdental plates are found in *Ceratosaurus* and the abelisauroid lineage. The issue of contention here centers upon whether the condition is present in *Dilophosaurus*, as scored by Holtz (1998). The interdental plates are fully coalesced in the type (UCMP 37302) and at least one referred specimen (UCMP 37303) (Fig. 36A). The interdental plates in these specimens are also very low and nearly obscured in medial view by a lamina of the maxilla (see below). The interdental plates are widely separated from each other in TMM 43646-1 and in UCMP 77270, the largest specimen of *Dilophosaurus* known (Fig. 36B). The plates are also broadly exposed on the medial surface of the maxilla, unlike the condition in UCMP 37302 and 37303. It is puzzling that the interdental plates are not fused in both the ontogenetically youngest juvenile (TMM 43646-1) and only adult (UCMP 77270) individuals of this taxon known, but are firmly co-ossified in other immature individuals (UCMP 37302, UCMP 37303). The cause and implications for this discrepency are not addressed here, and I leave this character coded as missing data for *Dilophosaurus*.

99. Medial surfaces of maxillary interdental plates smooth (0), or heavily striated/ridged (1) (Sampson et al., 1996, 1998).

100. Maxillary interdental plates relatively tall, broadly exposed (0), or low and partially obscured by lamina of maxilla (1) in medial view (modified from Carrano et al., 2002).

The maxillary interdental plates of most basal theropods are broadly exposed in medial view. The plates are dorsoventrally short in some basal theropod taxa, including the tetanurans *Baryonyx* and *Eustreptospondylus*, and the abelisauroid *Masiakasaurus*. The condition in *Dilophosaurus* is variable. A medial lamina of the maxilla is present medial to the fused interdental plates in UCMP 37302 and UCMP 37303, partially obscuring them in medial view (Fig. 36A). Contrasting this condition is the presence of dorsoventrally tall interdental plates in other specimens referred to *Dilophosaurus* (TMM 43646-1, UCMP 77270) (Fig. 36B). I code this character as missing data in the taxon.

101. Mesial dentary teeth similar in size (0), or enlarged (1) relative to mid- and distal dentary teeth (Rauhut, 2003).

The mesial and middle dentary teeth of most theropods are roughly equal in size, with a reduction of overall tooth size in the distal (posterior) direction. The mesial teeth are the largest in the dentary in *Dilophosaurus*, *Syntarsus rhodesiensis*, *"Syntarsus" kayentakatae*, *Masiakasaurus*, *Baryonyx*, *Suchomimus*, and reportedly also in *Eustreptospondylus* (Rauhut, 2003). The presence of an enlarged, fang-like tooth in the dentary was cited as a potential character by Gauthier (1986), Rowe (1989), and Rowe and Gauthier (1990). It is now clear that there is more than one enlarged mesial tooth in the dentary of coelophysoid taxa. CT imagery of the type skull of *"Syntarsus"*

kayentakatae (MNA V2623) shows that the anterior tip of the dentary is expanded and the first four dentary teeth are larger than the rest in the dentary. Most of the known skulls of *Coelophysis* have mandibles that are tightly closed on the skull, preventing this feature from being easily seen. I leave this character scored as missing data for *Coelophysis*.

Post-cranial Characters

102. Anterior articular surfaces of cervical and anterior dorsal centra flat or weakly concave (0), or strongly convex, ball-like (1) (Gauthier, 1986).

The terms 'amphicoelous' and 'opisthocoelous' were often used in earlier works to describe the overall morphology of the cervical and anterior dorsal vertebrae in theropods and other reptiles. Romer (1956) defined an amphicoelous centrum as being deeply concave at both ends, whereas an opisthocoelous centrum has a convex, ball-like anterior articular surface and a deeply concave, cup-like posterior articulation. Truly opisthocoelous vertebrae are present in a number tetanuran taxa, including *Torvosaurus*, *Eustreptospondylus*, and *Allosaurus*. The cervical centra of some taxa, such as *Dilophosaurus*, *Ceratosaurus*, and abelisaurids, have nearly flat anterior articular surfaces on their cervical centra and deeply concave posterior articulations. This form does not fit the definition of an opisthocoelous centrum sensu Romer (1956). Likewise, the anterior articular surface on the cervical vertebrae of some coelophysoid theropods (e.g., TMM 43689-18) is nearly flat, which does not fit the description of an amphicoelous centrum sensu Romer (1956). I therefore abandon the use of these

generalized terms of vertebral centrum structure in my character descriptions. The structure of each end of cervical vertebral centra appears to vary independently, and because of this each articular surface is evaluated as its own character.

103. Posterior articular surfaces of cervical and anterior dorsal centra flat or weakly concave (0), or deeply concave (1) (Gauthier, 1986).

The posterior articular surfaces of the cervical centra are weakly concave in the proximal outgroups to Theropoda. As mentioned above the posterior centrum articulation is deeply concave and cup-like in *Dilophosaurus*, *Ceratosaurus*, abelisaurids, and basal tetanurans (Fig. 37A). Cervical centra with deeply concave posterior ends were scored as present in *Abelisaurus* and *Noasaurus* by Carrano et al. (2002), yet there is no published record of cervical or anterior dorsal centra for either taxon.

The mid-cervical centra of *Coelophysis*, *"Syntarsus" kayentakatae*, *Syntarsus rhodesiensis*, and the Shake-N-Bake taxon are at least three times longer than the height of the anterior articular surface. The posterior articular surface of the centrum is deeply concave in the Shake-N-Bake taxon (Fig. 37B). The great length versus height of the vertebral centra (greater than four times anterior centrum height, see TMM 43689-18) in this taxon dictates that the depth of the articular surface is small relative to centrum length. There is simply not much distance over which the posterior articular surface can arc, and the illusion of a shallowly concave posterior surface may result. If the centrum height and degree of posterior concavity are kept constant, but the length of the centrum is reduced to approximately twice the anterior height of the centrum, the posterior surface

would be interpreted as being as deeply concave as in *Dilophosaurus*, *Ceratosaurus*, and tetanurans.

The cervical centra of *Coelophysis* were described as amphicoelous (Colbert, 1989), and the structure of the cervical vertebral articulations was scored as such in subsequent analyses (Holtz, 1998; Carrano et al., 2002; Rauhut, 2003). Some vertebrae referred to *Coelophysis* (TMM 45559-8, TMM 45559-13) bear posterior ends that are obviously concave (Fig 37C), albeit not as deeply so as seen in the Shake-N-Bake taxon. I score a deeply concave posterior surface of the centrum as present in *Coelophysis*.

The condition in *Syntarsus rhodesiensis* is uncertain. The term amphicoelous was used to describe the articular surfaces of the cervical centra. I was unable to find illustrations or photographs adequate to verify the structure of the posterior surface of the cervical centra in this taxon. I leave this character scored as missing data for this taxon. The condition in *"Syntarsus" kayentakatae* is only a little better known. The type (MNA V2623) is the only prepared specimen that preserves the cervical series, and the cervical vertebrae are all either articulated or matrix covers the posterior articular surface. The posterior end of the first dorsal vertebra is partially exposed in the specimen. The surface is concave, but it does not appear to be as deeply excavated as the mid-cervicals of *Dilophosaurus* and the Shake-N-Bake taxon. I leave this character scored as missing data in *"Syntarsus" kayentakatae*.

104. Anterior articular surfaces of anterior cervical centra circular or taller than wide (0), or wider than tall (1) (Gauthier, 1986; Rauhut, 2003).

105. Post-axial cervical vertebrae without (0), or with (1) pleurocoels in anterior part of centrum (modified from Gauthier 1986; Rowe, 1989; Rowe and Gauthier, 1990).

I use the term 'pleurocoel' to pertain to a clearly defined fossa, or also a foramen providing communication to an internal cavity, in the lateral surface of a vertebral centrum. Evidence continues to accumulate that these features are the osseous trace of pneumatic tissue that once contacted, invaded, and remodeled the vertebrae of saurischian dinosaurs (Britt, 1993, 1997; Wedel, 2003). The vertebral centra of *Herrerasaurus* and basal sauropodomorphs sometimes bear ovoid depressions near the neurocentral suture that might be the traces of such tissue. These depressions are indistinct and lack clear definition in most cases, so I do not consider them true pleurocoels.

All theropod taxa that possess cervical pleurocoels have one on each side of the anterior half of the centrum. It varies in size and shape from a large round opening as is present in the posterior cervicals of *Allosaurus* (Fig. 38A), to a small ovoid foramen such as in the anterior cervicals of *Carnotaurus* (Fig. 38B), to a deep but blind fossa as in *"Syntarsus" kayentakatae* and other coelophysoids (Fig. 38C). In most cases the pleurocoel is positioned in close proximity to the parapophysis, either posterodorsal to it or directly dorsal to it. The pleurocoel is more separated from the parapophysis in abelisaurids and *Masiakasaurus* (Fig. 38B, D). The pleurocoel tends to excavate the posterior base of the parapophysis in coelophysoid taxa, including *Coelophysis*, *Dilophosaurus*, *"Syntarsus" kayentakatae*, and the Shake-N-Bake taxon (Fig. 38C). The

anterior pleurocoel can be almost hidden from view by the transverse process of the vertebra and the tuberculum of the cervical rib in those specimens in which these components are preserved (Fig. 38C).

106. Post-axial cervical vertebrae without (0), or with (1) pleurocoels in posterior part of centrum (modified from Gauthier 1986; Rowe, 1989; Rowe and Gauthier, 1990).

There is a second pleurocoel present in the cervical centra of coelophysoids, *Elaphrosaurus*, *Ceratosaurus*, abelisaurids, and at least some specimens of *Masiakasaurus* (Fig. 38B-D). It all these cases it is located posterior to the more anterior pleurocoel, and often in the same horizontal plane (Fig. 38B-D). The posterior pleurocoel is usually larger than its anterior counterpart, sometimes excavating the lateral surface of the centrum to nearly its ventral margin in specimens of *Coelophysis* (AMNH 7223, AMNH 7228, TMM 45559-8, TMM 45559-13), and the Shake-N-Bake taxon.

The distribution of the posterior pleurocoel in the cervical series may vary among coelophysoids. There are no posterior pleurocoels in cervicals eight through ten of the holotype of *"Syntarsus" kayentakatae*. There are posterior pleurocoels in the posterior cervicals of *Coelophysis*, and the Shake-N-Bake taxon. It is unclear from descriptions whether or not the posterior cervical vertebrae of *Syntarsus rhodesiensis* possess posterior pleurocoels or not (Raath, 1977).

107. Cervical pleurocoels absent (0), or present as deep ovoid fossae or pockets (1), or present as foramina leading to internal centrum cavities (2). (UO)

The cervical vertebrae of coelophysoid theropods are distinct in the form of their pleurocoels. There are two pleurocoels on each side of the vertebral centrum as with *Elaphrosaurus*, *Ceratosaurus*, and some abelisaurs. Both pleurocoels open broadly and form deep ovoid fossae or pockets in the lateral surface of the centrum (Fig. 39A-C). This contrasts sharply with the condition in *Ceratosaurus*, abelisaurs, and tetanurans in which the pleurocoels are foramina that provide access to larger cavities in the centrum interior. The pleurocoels from the right and left sides may invade the centrum so deeply that they are separated only by a median septum (Fig. 39B, C). The walls of the fossae are not perforated by additional foramina in most cases, and there is no communication with other cavities within the narrow confines of the remaining parts of the centrum. The exception may be in some vertebrae of *Dilophosaurus* (UCMP 37302), which may also have foramina deep within the pleurocoel. The anterior pleurocoel may deeply invade the base of the parapophysis and hollow out much of the centrum immediately behind the anterior articular surface. This closely parallels the condition present in some basal sauropods, a vertebral pneumatic morphology labeled procamerate by Wedel (2003) (Fig. 39A-C).

The posterior pleurocoels of *Dilophosaurus* are large ovoid depressions in the lateral surface of the centrum (Figs. 39A, 40A). The posterior pleurocoels of *Coelophysis* (AMNH 7223, AMNH 7228, TMM 45559-8, TMM 45559-13) and *Syntarsus rhodesiensis* are more elongate, with well-defined, rounded posterior borders and less distinct anterior margins (Fig. 40B). The pleurocoels are very deep, blind recesses in the type of *"Syntarsus" kayentakatae* (Figs. 39B, 40C). The cervicals of the Shake-N-Bake

taxon are unique in that the posterior pleurocoel has a broad fossa as found in *Coelophysis* and *Syntarsus rhodesiensis*, but there is also a secondary recess within in the fossa that deeply invades the centrum (Figs. 39C, 40D). The right and left side recesses within the pleurocoel are separated on the midline by only a thin septum (Fig. 39C). There appears to be little or no room for large internal cavities (=centrocoels sensu Welles, 1984) in the cervicals of most of these taxa, because much of each centrum's volume is consumed by pleurocoels.

The cervical vertebrae of *Elaphrosaurus* are similar to those of coelophysoids in several respects, including morphology of the pleurocoels (Fig. 40E). The posterior pleurocoel is a large, well-defined fossa that resembles the condition in *Dilophosaurus*. Rauhut (2003) claimed there are additional foramina within the cervical pleurocoels that access the centra in this taxon, but I am unable to verify this in original illustrations (Janensch, 1925) or photographs of the specimen (courtesy of P. Makovicky, 1997).

Cervical pleurocoels take the form of foramina that access internal centrum cavities (centrocoels) in *Ceratosaurus*, abelisaurids, and tetanurans. There is a variable number (from zero to two) of foramina penetrating the centrum in the three cervical vertebrae known for *Masiakasaurus* (Carrano et al., 2002). Illustrations clearly show that one of the vertebrae (FMNH PR 2140) is devoid of centrum fossae or foramina, while another (FMNH PR 2141) is punctured by two large openings arranged in anterior and posterior positions on the centrum (Fig. 38D). It was claimed that, "potentially pneumatic fossae are entirely lacking; therefore these foramina are interpreted as vascular and non-pneumatic" (Carrano et al., 2002:515). The pleurocoel foramina in the cervicals

of *Ceratosaurus* and tetanurans also lack additional fossae excavated around them on the centrum surface, yet these apertures are regularly interpreted as pneumatic in nature. There is no other evidence given to support assignment of these openings in the cervicals of *Masiakasaurus* to a strictly vascular function. I consider these openings pleurocoels homologous to those in *Ceratosaurus*, abelisaurids, and tetanuran theropods.

108. Internal pneumatic cavities in vertebral centra absent (0), or present with camerate structure (1), or present with camellate structure (2) (Carrano et al., 2002). (UO)

Terminology applied to the osseous traces of archosaur vertebral pneumaticity was formulated by Britt (1993, 1997), and expanded upon by Wedel (2003). Using these works as guides, a vertebra is considered 'camerate' if the centrum houses an internal cavity or cavities that are relatively rounded, with thick-walls, and may be subdivided into only a few chambers that are approximately regular in their distribution within the centrum. A 'camellate' centrum is typified by more angular internal cavities with thin walls, delicate internal sepatae, and usually much smaller and irregularly distributed subdivisions.

It was stated by Britt (1997) that non-tetanuran theropods possessed camerate vertebrae, whereas almost all tetanurans had camellate vertebral centra. In contrast with this statement, recent cladistic analyses of basal theropods (Carrano et al., 2002; Rauhut, 2003) were in agreement in coding several basal tetanuran taxa (including *Allosaurus* and *Torvosaurus*) as having camerate cervical vertebral centra, whereas several non-tetanuran theropods (*Ceratosaurus*, abelisaurids) were coded as having camellate cervical centra.

These analyses also identified and scored camarate cervical centra as present in *Coelophysis* and other coelophysoid theropods, a conclusion consistent with the findings of Britt (1993, 1997).

It was pointed out by Britt (1997) that a hollow bone does not in itself indicate the presence of pneumaticity, because the internal spaces of bones may also be filled with marrow or other fatty deposits. An external communication must also be present to connect the bone interior with the bone exterior, and allow pneumatic tissue to enter the bone and fill the cavity. The lateral surfaces of many coelophysoid cervical centra are marked by ovoid recesses (pleurocoels) that invade the centrum so deeply that right and left side recesses are sometimes separated by only a thin median septum. There are no foramina or other apertures to allow communication between these deep pneumatic recesses and the centrum interior. Whatever cavity might exist within the limited space between the pneumatic recesses could not be pneumatic in function. Therefore, pneumatic internal centrum cavities are scored as absent in *Coelophysis*, "*Syntarsus*" *kayentakatae*, the Shake-N-Bake taxon, and *Dilophosaurus*. A possible exception might be one cervical centrum of *Dilophosaurus* that bears a probable foramen within one of its centrum pneumatic recesses, but there is no consistent distribution of such foramina in this taxon. *Liliensternus liliensterni* was also coded as possessing camerate vertebral centra by Carrano et al. (2002), but then coded as lacking internal pneumatic cavities by Rauhut (2003). The latter assessment seems appropriate, given the absence of foramina to allow passage of pneumatic tissue to the centrum interior in the known and figured cervicals of *Liliensternus*.

109. Transverse processes of postaxial presacral vertebrae without ventral braces (0), or ventrally braced by centrodiapophyseal laminae (1).

110. Cervical epipophyses absent (0), or are low ridges (1), or elongate, narrow, and project posterolaterally beyond postzygapophyses (2), or strongly developed, and project mostly dorsally above zygapophyses (3) (Holtz, 1994, 1998; Novas, 1997). (UO)

Epipophyses are present on the cervical vertebrae of *Herrerasaurus*, sauropodomorphs, *Eoraptor*, and all other theropods. The morphology of the epipophyses varies among taxa. The epipophyses are little more than raised rugosities on the dorsal side of the postzygapophyseal projections in *Herrerasaurus*, *Eoraptor*, and basal sauropodomorphs. They do not extend posteriorly beyond the rim of the postzygapophyses in these taxa.

The cervical epipophyses are raised well above the surface of the postzygapophysis in *Dilophosaurus*, *Coelophysis*, *Syntarsus rhodesiensis* and *"Syntarsus" kayentakatae*. They are mediolaterally narrow processes above and posterior to the postzygapophyseal facet in *Dilophosaurus* (Fig. 41A, B). The cervical epipophyses project farther posteriorly in *"Syntarsus" kayentakatae* and they are dorsoventrally flatter, but this may be the result of post-mortem distortion in the type specimen (Fig. 41C, D). Rauhut (2003) indicated the epipophyses are absent or weakly developed in the cervicals of *Liliensternus*, and I follow his evaluation of epipophyseal

morphology in the taxon. There are several partial cervical vertebrae of the Shake-N-Bake taxon known, but the postzygapophyses are broken off on all of them, prohibiting evaluation of this character.

The cervical epipophyses are strongly developed in *Ceratosaurus*, abelisaurids and most basal tetanuran taxa (Fig. 42A-D). Unlike the condition in the coelophysoids, the epipophyses in these taxa are more dorsally directed instead of posterolaterally. The epipophyses are far larger in *Allosaurus* and abelisaurids than in *Ceratosaurus*, and they also project posteriorly well beyond the margins of the postzygapophyses (Fig. 42B-D). The epipophyses are also very robust in section instead of the more rod-like structures in many coelophysoids. The epipophyses on the cervicals of *Dilophosaurus* approach but do not equal the robust morphology present in these taxa.

111. Cervical epipophyses not anteriorly expanded (0), or with anteriorly directed processes (1) (Sereno, 1999a; Carrano et al. 2002).

112. Cervical epipophyses at level below or even with top of neural spine (0), or dorsal to top of neural spine (1) (modified from Holtz, 1998).

The epipophyses on the cervical vertebrae of most theropods fail to ascend to a level even with the top of the vertebral neural spine. This is the case even among *Ceratosaurus* and tetanurans that have large cervical epipophyses. Abelisauroids are distinctive in the remarkable degree of dorsalward extension of the epipophyses above

the top of the neural spine (Fig. 42C, D). This morphology is not strictly related to size, as shown by its presence in the diminutive taxa *Masiakasaurus* and *Noasaurus*.

113. Cervical vertebrae without (0), or with (1) epipophyseal-prezygapophyseal laminae (Coria and Salgado, 1998).

114. Axis lacks pleurocoels (0), or bears pleurocoels (1) (Rowe, 1989).

The polarity of this character is reversed from its original usage (Rowe, 1989; Rowe and Gauthier, 1990). There are no pleurocoels in the axial vertebra of most archosaurs, including the proximal outgroups to Theropoda and coelophysoids (Fig. 43A). In the present analysis, axial pleurocoels are unequivocally present only in *Ceratosaurus*, *Carnotaurus*, *Majungatholus*, *Baryonyx*, and *Allosaurus* (Fig. 43B, C). Pleurocoels were coded as present in the axis of *Torvosaurus* by Carrano et al. (2002). The axis of *Torvosaurus* was not known at the time of the most recent description of the taxon (Britt, 1991), and no source or specimen number was cited to support scoring this feature as present in the taxon (Carrano et al., 2002). The character is scored as missing data for *Torvosaurus*.

115. Axis bears a distinct diapophysis (0), or lacks a distinct diapophysis (1) (Rowe, 1989).

The second cervical of most dinosaur taxa bears at least rudimentary transverse processes with small diapophyseal facets at their terminus. Coelophysoids are unusual in

the complete lack of axial transverse processes. The well-preserved atlas-axis complex of the type of *Dilophosaurus* illustrates the derived condition very well (Fig. 43A, 44). Axial transverse processes and diapophyseal facets are also absent in *Coelophysis*, *Syntarsus rhodesiensis*, and *"Syntarsus" kayentakatae*.

116. Axial parapophysis distinct, strongly developed (0), or weakly developed to indiscernible (1) (Rowe, 1989).

The axis bears a prominent parapophysis in sauropodomorphs, *Herrerasaurus*, and most theropods (Fig. 43B, C), but not in the basal ornithischian *Lesothosaurus*. The axis of the coelophysoids *Dilophosaurus*, *Coelophysis*, *"Syntarsus" kayentakatae* and *Syntarsus rhodesiensis* lack an easily discernable parapophyseal facet (Fig. 43A, 44). This is somewhat surprising because of the unquestionable presence of axial ribs in some of these taxa.

117. Axial neural spine and epipophyses/postzygapophyses connected by laminae (0), or widely separated (1) (modified from Sereno et al., 2004).

118. Anterodorsal border of axial neural spine straight-edged or weakly concave (0), or dorsally convex and blade-like (1) (Makovicky and Sues, 1998; Tykoski, 1998).

The axial neural spine is raked sharply in the posterodorsal direction in *Marasuchus*, *Herrerasaurus*, *Lesothosaurus*, basal sauropodomorphs, and most basal tetanuran taxa (Fig. 43C). The dorsal margin of the spine usually bears a straight edge, or

is weakly concave anterodorsally in these taxa. The axial neural spine can also be rod-like in structure, especially in some tetanurans. A very different morphology is present in *Dilophosaurus*, *Coelophysis*, *"Syntarsus" kayentakatae*, *Syntarsus rhodesiensis*, *Ceratosaurus*, and *Carnotaurus*. In these taxa the spine is anterodorsally expanded and blade-like, and usually bears an anterodorsally convex margin in lateral view (Figs. 41C, 43A, B, 44). The latter condition was also reported in the tetanuran *Eustreptospondylus* (Rauhut, 2003).

119. Axial neural spine stops posterior to prezygapophyses (0), or extends anteriorly beyond prezygapophyses (1).

The anterior tip of the axial neural spine usually terminates just posterior to a plane through the anterior rim of the axial prezygapophyses in most dinosaur taxa. This is especially true in those taxa with posteriorly directed, narrow axial neural spines (Fig. 43C). The exception in this analysis is the dinosauriform *Marasuchus*, in which the neural spine is posterodorsally oriented, but still reaches anteriorly beyond the margins of the prezygapophyses. The axial neural spine extends beyond the prezygapophyses in coelophysoids, *Ceratosaurus*, and *Carnotaurus* (Fig. 41C, 43A, B, 44). The condition of the axial spine in *Eoraptor* cannot be determined from the cast available.

120. Axial neural arch lacks pneumatic foramina (0), or with pneumatic foramen/foramina posterodorsal to diapophysis (1).

This character is currently confirmed only in *Ceratosaurus* and *Carnotaurus*. The axial neural arch is perforated by a large foramen posterodorsal to the diapophysis in both of these taxa (Fig. 43B, C). The axis is not described for any other abelisauroid. Relatively complete skeletons of the abelisaurids *Aucasaurus* and *Majungatholus* are now known, and these should help resolve whether this character (and many others) is diagnostic for a *Ceratosaurus* + abelisauroid clade. The axial neural arch of *Allosaurus* is also penetrated by a foramen in this relative position, but such a feature is not known in the more basal tetnauran taxa in this analysis.

121. Anterior post-axial cervical centra with rounded or flattened ventral surface (0), or median ventral keel (1) (Makovicky, 1995; Rauhut, 2003).

122. Post-axial cervical prespinal fossae narrow (0), or broad (1) (Coria and Salgado, 1998).

123. Neural spines of post-axial cervicals dorsoventrally high (0), or low (1) (Russell and Dong, 1993; Carrano et al., 2002).

124. Neural spines of post-axial cervicals anteroposteriorly broad (0), or very short (1) (Carrano et al., 2002).

125. Cervical zygapophyses positioned near midline (0), or displaced far laterally away from centrum (1) in dorsal view (Makovicky and Sues, 1998; Holtz, 1998).

126. Post-axial cervical neural arches solid (0), or house pneumatic cavities lateral to neural canal (1).

A cavity within a bony element is considered potentially pneumatic in origin and function only if it has an obvious communication with the exterior of that element, and if it has some modern homologue in extant Archosauria. The body of each cervical neural arch between the neural canal and the lateral surface of the arch (=neural arch pedicle) is solid in *Marasuchus*, basal ornithischians, sauropodomorphs, *Herrerasaurus*, *Eoraptor*, and *Dilophosaurus*.

The neural arches of several coelophysoid and ceratosauroid taxa are pierced by foramina or other apertures (Fig. 45A-C). The cavities within the cervical neural arches of *Coelophysis*, the indeterminate tetanuran *Coelurus fragilis*, and the ornithomimid tetanuran *Struthiomimus altus* were described at length by Colbert (1989). The arch cavities were identified as 'pleurocoels' (Colbert, 1989), but I restrict use of that term to pneumatic fossae, foramina, and cavities of the vertebral centrum. There are reportedly two apertures accessing the arch cavity on both sides of each cervical neural arch of *Coelophysis* (Colbert, 1989:figs. 50, 52). The anterior opening is posterior to the anterior rim of the arch at about the same level as the neural canal. The posterior opening is anterior and lateral to the posterior rim of the neural arch. Both apertures are

dorsoventrally taller than mediolaterally wide, with a slightly triangular outline in lateral view.

The same type of opening is present near the posterior rim of the cervical neural arches of *"Syntarsus" kayentakatae* and the Shake-N-Bake taxon (Figs. 45A, B). These taxa do not have an anterior aperture leading to the arch cavities, so the anterior openings reported in the cervicals of *Coelophysis* appear apomorphic for the taxon. Broken specimens of the Shake-N-Bake taxon (TMM 43689-21) and *"Syntarsus" kayentakatae* (MNA V2623-fifth cervical vertebra) clearly show the cavities lateral to the neural canal, separated from it by only a thin lamina. It is unknown if similar cavities and apertures are present in *Syntarsus rhodesiensis* because figures and photographs of the cervicals of this taxon are not sufficiently detailed to be certain.

The cervical neural arches are extensively pneumatized in abelisauroid theropods. Multiple foramina perforate the neural arch within the infrapostzygapophyseal fossa in *Masiakasaurus* (Carrano et al., 2002:fig. 7A), and at least one large foramen is present on the dorsal surface of the arch anterior to the neural spine in the same specimen (FMNH 2140). The cervical arches of *Carnotaurus* are pierced by multiple foramina within the major arch fossae (Fig. 45C), and openings may be present in the cervicals of *Majungatholus* (Sampson et al., 1998). *Ilokelesia* has a large foramen penetrating the arch wall anterior to the postzygapophysis (Coria and Salgado, 1998). It is assumed that all these foramina lead to cavities within the arch pedicle.

127. Lateral surface of post-axial cervical arch pedicels solid (0), or pierced by foramen/foramina anteroventral to postzygapophysis (1), or bear triangular, posterior-directed apertures anterior to postzygapophysis (2). (UO)

The opening that provides access to cavities within the cervical neural arches of some basal theropods is variable. The major differences are noted in the description of the preceding character. The cervical neural arch cavities of some taxa, such as *Carnotaurus*, *Ilokelesia*, and *Masiakasaurus* are entered through a large foramen or foramina that pierce the wall of the neural arch (Fig. 45C). These foramina generally face laterally or posterolaterally so that the openings are easily visible in lateral or posterolateral view.

The cervical neural arch cavities present in some coelophysoid taxa are entered through an opening on the lateral surface of each neural arch pedicle. The apertures open posteriorly, and have a triangular to nearly rectangular outline in posterior view (Fig. 45A, B). The aperture on a given side is difficult to recognize in lateral view because of the posterior-facing orientation of the opening. This apomorphic condition is present in *Coelophysis*, *"Syntarsus" kayentakatae*, and the Shake-N-Bake taxon. Its presence in *Syntarsus rhodesiensis* is suspected but not confirmed. Such openings are not present in *Dilophosaurus*.

128. Mid-cervical centrum length <3 times (0), or 3<4 times (1), or ≥4 times (2) diameter of anterior face (modified from Holtz, 1998; Sereno, 1999a). (O)

For the purposes of this and subsequent characters the 'mid-cervicals' are recognized as the fourth through seventh vertebrae. Most theropods have cervical vertebral centra that are approximately twice as long as the diameter of the anterior rim of the centrum. A number of coelophysoids have mid-cervicals that are approximately three or more times as long as the diameter of the anterior articular face. These include *Coelophysis*, *"Syntarsus" kayentakatae* (Fig. 46A), *Syntarsus rhodesiensis*, and the Shake-N-Bake taxon (Fig. 46B). Interestingly, the same condition is present in *Elaphrosaurus* (Fig. 46C).

Elongation of the mid-cervical centra is taken even further in *Elaphrosaurus* and the Shake-N-Bake taxon. Each has at least some mid-cervicals with centra four or more times longer than their anterior diameter (Fig. 46B, C). A previous phylogenetic analyses found these taxa were not closely related (Tykoski, 1998), a finding supported in the pre-test analyses conducted in the present work. It is therefore probable that this vertebral feature is homoplastic beteen these two taxa. However, there are a number of apomorphies in the skeleton of *Elaphrosaurus* that are shared with coelophysoid taxa. It remains possible that an analysis might eventually find *Elaphrosaurus* to be allied more closely to *Coelophysis* than *Ceratosaurus*. It is for this reason that this derived character state is included in this present analysis.

129. Cervical neural spines approximately centered over centrum (0), or positioned mostly over anterior half of centrum (1) (Carrano et al., 2002).

130. Cervical ribs remain separate from (0), or co-ossify to (1) their respective vertebral centra in adults (Gauthier, 1986).

Fusion of the cervical ribs to their respective vertebrae was also used as a character in the ontogenetic analysis (see Chapter 1). However, this character is not strictly controlled by ontogeny. The condition is not present in most basal sauropodomorphs, but it is present in adults of some Sauropoda. The cervical ribs are not fused to the vertebrae in adults of most basal tetanuran taxa. The character is widely distributed among those coelophysoids known from adult material, some specimens of *Ceratosaurus*, and abelisauroids. The only specimen of *Dilophosaurus* known from relatively advanced ontogenetic material (UCMP 77270) does not have cervical ribs fused to their vertebrae, and for now this character is coded as absent in the taxon.

Not all the cervical ribs fuse to vertebrae in those taxa that exhibit this character. The holotype of *"Syntarsus" kayentakatae* (MNA V2623) is the skeleton of an adult individual that preserves all the cervical ribs in articulation or close association. The first three cervical ribs are not fused to their respective vertebrae (Fig. 41C). Cervical ribs four through seven are completely fused with the parapophyses and diapophyses of their vertebrae (Figs. 45A, 46A). The eighth cervical rib may not be fully fused to the diapophysis, and it is unknown if it is fused with its parapophysis. There is no co-ossification of the ribs to the ninth and tenth cervical vertebrae.

131. Cervical ribs stout, relatively blade-like (0), or exceptionally thin posteriorly (styliform) (1) (Tykoski, 1998; Holtz 1998).

132. Cervical ribs <4 (0), or ≥4 (1) times centrum length (Tykoski, 1998; Holtz 1998).

133. Cervical rib heads without signs of pneumaticity (0), or are marked by pneumatic excavations (1) (Harris, 1998; Carrano et al., 2002).

134. Anterior cervical rib shafts proximal part rod-like or blade-like (0), or greatly expanded and flattened (1) (Coria and Salgado, 1998).

135. Cervical and dorsal neural arch surfaces ventral to transverse processes are imperforate (0), or pierced by multiple pneumatic foramina (1).

Some abelisauroid taxa possess cervical vertebrae with a foramen or foramina penetrating the lateral surfaces of the neural arch anterior to the postzygapophyses (see above). There are additional foramina located within the other infradiapophyseal fossae of some cervical and dorsal vertebrae in *Carnotaurus*, *Masiakasaurus*, and the partial third(?) cervical of *Ilokelesia* (Bonaparte et al., 1990; Coria and Salgado, 1998, Carrano et al., 2002) (Fig. 47). The neural arches of the coelophysoids and basal tetanurans in this study lack accessory foramina in the vertebral arches. Only a single cervical vertebra was figured for *Majungatholus* (Sampson et al., 1998), and the presence or absence of accessory foramina in the neural arch can not be determined from the illustration.

136. Anterior dorsal vertebrae without (0), or with (1) pleurocoel in anterior half of centrum (Holtz, 1994, 1998).

Pleurocoels are present in at least the anterior dorsal vertebrae of many theropods. Pleurocoels are apparently restricted to the anterior-most two to three dorsal vertebrae of coelophysoids. The pleurocoel retains the same morphology as the anterior pleurocoels of the cervical series in that it is a deep pocket excavated into the centrum and the posterior surface of the parapophysis (Fig. 48A). The cavity opens posterolaterally, and is difficult to see in lateral view (Fig. 48B). The anterior dorsals of *Carnotaurus*, *Xenotarsosaurus*, and tetanurans have a foramen in their anterior parts that lead to cavities within the dorsal centrum. These pleurocoels differ from the coelophysoid type in that they open laterally, and do not appear to excavate and invade the posterior side of the parapophysis (Fig. 48C).

137. Dorsal vertebrae with parapophyses on or close to centrum (0), or with parapophyses that project laterally on "stalks" (1) (Carrano et al., 2002).

138. Hyposphene-hypantrum articulations absent (0), or present (1) on dorsal vertebrae (Gauthier, 1986).

139. Dorsal transverse processes directed laterally, giving rectangular profile in dorsal view (0), or with strongly backswept anterior margin resulting in triangular profile in dorsal view (1) (modified from Rowe, 1989; Rowe and Gauthier, 1990).

This and the following character are derived from a single character first used by Rowe (1989) and Rowe and Gauthier (1990). They recognized that many of the dorsal vertebrae in coelophysoid taxa are approximately triangular in dorsal view, a condition not usually found among other theropods. However, the character is problematic in that it has been broadly interpreted through several cladistic analyses, or poorly understood. The validity of this feature was questioned by Rauhut (2003), who removed it from consideration in his analysis. The reasons given for discarding this character were that the transverse processes are more or less triangular in dorsal view in the majority of saurischians, and the degree to which the transverse processes are backswept varies through the dorsal series and may be individually variable. I argue that these criticisms were without merit.

The claim that dorsal transverse processes are "more or less triangular in the majority of saurischians" (Rauhut, 2003) can only be supported if the even slightest distalward taper of the process is determined to result in a triangular profile. This ignores details of the morphology present in the transverse processes of coelophysoids, *Ceratosaurus*, and possibly other taxa that are absent in most other theropod and non-theropod taxa. Examples of three non-ceratosaur taxa that have backswept, triangular dorsal transverse processes were cited by Rauhut (2003). These included *Plateosaurus*, *Sinraptor dongi* (Currie and Zhao, 1993), and *Gallimimus bullatus* (Osmolska et al., 1972). It was claimed that the transverse processes are no less triangular in these three taxa than in *Ceratosaurus* or abelisaurids.

There are no illustrations of the dorsal vertebrae in dorsal or ventral views provided in the description of *Sinraptor*. Lateral-view figures show that the transverse processes may be strongly backswept in most of the dorsal vertebrae. I cannot confirm this at this time, and it was not stated by Rauhut (2003) whether or not the specimen was personally examined.

The transverse processes in *Gallimimus* are roughly triangular in dorsal view, but do not exhibit the sharply raked, straight-edged profile present in the dorsals of many coelophysoids and *Ceratosaurus* (Osmolska et al., 1972; Britt, 1991:fig. 25C). The anteroposterior breadth of the transverse processes is also far less than seen in the latter taxa, a point discussed below.

Without illustration of the dorsal vertebrae of the *Plateosaurus* specimens cited by Rauhut (2003) (GPIT I, MB XXV), it is not possible to verify the morphology of the transverse processes in the specimens at this time. However, photographs of other *Plateosaurus* specimens show a range of dorsal transverse process shapes, including triangular (AMNH 6810) and very rectangular (SMNS 58958) profiles (Galton, 2001a:fig. 1d, pl. III-fig. 2). Other prosauropod dorsals have rectangular dorsal transverse processes (TMM 42179-20) (Fig. 49A), while others have backswept process that retain a rectangular form (AMNH 5624) (Galton, 1976:fig. 4).

The presence of triangular transverse processes on the dorsal vertebrae of the three aforementioned taxa does not invalidate the usefulness of the character in phylogenetic analyses, contrary to Rauhut (2003). These taxa are only very distantly related, and none of their proximal outgroups or common ancestors possess the feature in

question. If triangular transverse processes on the dorsal vertebrae are present in them, the presence of these structures represents an autapomorphic character in each taxon and should not be construed as evidence for a broad distribution of triangular transverse processes across Saurischia.

It shold not be surprising that the triangular transverse processes on the dorsal vertebrae vary in profile along the dorsal column of an individual, and among individuals of the same taxon. No terrestrial tetrapod exhibits morphological invariability along the vertebral column. It is illogical to conclude that a character expressed in some of the vertebral series is not valid for the purpose of cladistic analysis simply because it is not present in all adjacent vertebrae. Transverse process form does vary along the dorsal series in all the coelophysoid specimens in this analysis, but that is normal for nearly all morphological structures in common along a vertebral column. The character description provided by Rowe (1989) and Rowe and Gauthier (1990) does not require that every dorsal transverse process in every individual of every evaluated taxon be perfectly triangular profile in dorsal view.

Ceratosaurus and abelisaurids were specifically cited by Rauhut (2003) as taxa that bore the triangular form of the dorsal transverse processes, and yet he still considered this character non-informative for the purpose of phylogeny reconstruction. The shared presence of triangular transverse processes on the dorsal vertebrae in coelophysoids, *Ceratosaurus*, and abelisaurids dictates the character should be included in a phylogenetic analysis, because it represents a potential synapomorphy. The a priori removal of this and other characters that at one time diagnosed Ceratosauria (sensu

Rowe, 1989) or other clades within it may represent selective elimination of characters that support alternative hypothesis of basal theropod phylogeny.

The character description first used by Rowe (1989) and Rowe and Gauthier (1990) was not specific enough to address the unique dorsal transverse process morphology in coelophysoids, *Ceratosaurus*, and perhaps abelisaurids. I break the character into two morphological constituents, because the triangular transverse processes in these taxa appear to be the result of at least two potentially independent variables. These are: (1) the strongly backswept, near-linear anterior margin of the transverse process; and (2) the extraordinary anteroposterior breadth of the transverse process along its proximal edge where it arises from the neural arch. The first of these variables is addressed here, and the second is evaluated in the following character.

The anterior margins of the dorsal transverse processes are angled posterolaterally to a high degree in a number of the ingroup taxa of this study. These include specimens referred to *Ceratosaurus* (BYUVP 4952) (Fig. 49B), *Dilophosaurus* (UCMP 77270, TMM 43646) (Fig. 49C, D), *Syntarsus rhodesiensis* (QG1) (Fig. 49E), and the Shake-N-Bake taxon (Fig. 49F). The condition in *Coelophysis* is debatable. Artistic reconstructions of some dorsal vertebrae of this taxon show nearly rectangular, slightly backswept, narrow transverse processes (Colbert, 1989:figs. 53, 55). Photographs and casts of some specimens (AMNH 7223, 7224) have several backswept, triangular transverse processes, especially in the anterior part of the series. I score this character present in *Coelophysis*.

Carnotaurus is the only abelisaurid for which relatively complete descriptions and illustrations of the dorsal vertebrae are known. The dorsal vertebral transverse processes are highly variable. None of the illustrated vertebrae have posterolaterally angled, straight-edged transverse processes, although at least some are broadly triangular in dorsal view (Fig. 49G). *Carnotaurus* and *Majungatholus* were both scored as having triangular transverse processes by Carrano et al. (2002). I code the derived state as absent in *Carnotaurus* and unknown in *Majungatholus*, but code the next character present in at least *Carnotaurus*.

140. Transverse processes of dorsal vertebrae anterposteriorly narrow (0), or broad, extending to lateral margin of prezygapophysis (1) (modified from Rowe, 1989; Rowe and Gauthier, 1990).

The other morphological variable that contributes to the triangular profile of the transverse processes on the dorsal vertebrae is the anteroposterior breadth of the process. The transverse process is relatively narrow and projects laterally from the neural arch beginning at a point posterior to the prezygapophyses in outgroups to Theropoda, as well as most tetanuran theropods (Fig. 49A, H). The transverse process arises from the lateral margin of the prezygapophyseal facet and continues posteriorly to the base of the postzygapophysis in many of the dorsal vertebrae of coelophysoids and *Ceratosaurus* (Fig. 49B-F). The vertebral centra are also long relative to their diameter in most of these taxa. This combination of features results in transverse processes that are unusually broad (Fig. 49B-F). The breadth of the process is evaluated along its proximal (medial)

part where it first arises from the neural arch. The breadth of the process is independent of whether or not the anterior margin is posterolaterally angled, shown by the width of the process in the abelisaurid *Carnotaurus* (Fig. 49G).

141. Posterior dorsal vertebral centrum length <1.33 (0), or ≥1.33 (1) times height of anterior articular surface (modified from Rauhut, 2003).

142. Posterior dorsal vertebral centrum length <2 (0), or ≥2 (1) times height of anterior articular surface (Sereno, 1999a).

143. Neural spines of posterior dorsal vertebrae no taller than anteroposteriorly long (0), or substantially taller than anteroposteriorly long (1) (Rauhut, 2003).

144. Vertebra 23 part of dorsal vertebral series (0), or incorporated into sacral series (as dorsosacral 3) (1).

Archosaurs ancestrally have two sacral vertebrae, the primordial or 'true' sacrals (Romer, 1956). This plesiomorphic condition persists in basal dinosauriforms such as *Marasuchus*, as well as *Herrerasaurus*. The composition (cervicals versus dorsals) and number of pre-caudal vertebrae in *Herrerasaurus* is not certain, because no specimen preserves the entire series (Novas, 1993; Langer, 2004). The vertebral count was assumed to mirror the condition described in basal ornithodirans, reportedly nine

cervicals, 15 dorsals, and two sacrals, for a total of 26 pre-caudal vertebrae (Fig. 50A) (Bonaparte, 1975).

There is no clear consensus among paleontologists as to the sequence by which vertebrae were incorporated into the sacral series of theropods, or even Saurischia. Most basal sauropodomorph taxa have sacra characterized by the addition of a third vertebra. There is some dispute over whether this addition is taken from the dorsal or caudal series (Galton, 1999, 2001b; Yates, 2003). The most basal and earliest sauropodomorphs known (*Thecodontosaurus antiquus* and *Saturnalia tupiniquim*) probably derived third sacrals from the caudal series, and hence have a S1 + S2 + cS1 sacrum (Langer et al., 1999; Benton, et al., 2000; Langer, 2003). The same morphology is present in *Plateosaurus* and many other sauropodomorph taxa (Fig. 50B). There appears to be a clade or clades of basal sauropodomorphs that have a dS1 + S1 + S2 sacrum (Galton, 1999, 2001b), but for now this condition is considered derived within Sauropodomorpha.

The identification of sacral homology becomes more confused within Theropoda. The sacral incorporation pattern descibed for *Allosaurus* (Madsen, 1976) was that of a single dorsosacral and two caudosacrals added to the ancestral two sacrals, for a dS1 + S1 + S2 + cS1 + cS2 pattern (Fig. 50C). The same interpretation of sacral homology was used by Molnar et al., (1990), Sereno (1999a) as a character diagnostic of his Neotheropoda), Carrano et al. (2002) as one of two derived character states encompassing sacal homology in theropods more derived than *Eoraptor* and *Herrerasaurus*, and Tykoski and Rowe (2004) in describing sacral homology in coelophysoid ceratosaurs.

An additional derived state was listed by Carrano et al. (2002) that was shared by *Elaphrosaurus*, *Ceratosaurus*, and abelisauroids. The homology of vertebral incorporation into the sacrum in these taxa was interpreted by Carrano et al. (2002) as dS3 + dS2 + dS1 + S1 + S2 + cS1 (Fig. 50D). Instead of two caudosacrals added to the ancestral true sacrals, only a single caudosacral was added, and three dorsal vertebrae were incorporated into the sacral series.

It is my opinion the interpretation of sacral homology which Carrano et al. (2002) viewed as a derived state in *Ceratosaurus* and abelisauroids is actually more reflective of the sacral homologies in Theropoda, and to an extent, Saurischia. The interpretation of two caudosacrals in theropods with a five-vertebra sacrum is incorrect. This is based upon examination of vertebral counts and the position of the sacral vertebrae in those taxa that preserve complete or nearly complete pre-caudal series. My hypothesis is also supported by mapping the distribution of these transformations on both previously plublished hypotheses of saurischian phylogeny and results from this analysis.

There is an unexpected trend in the vertebral count of basal sauropodomorphs and theropods. There are 28 pre-caudal vertebrae in those taxa known from specimens that preserve the pre-caudal series, and the true two sacrals are the 26th and 27th in the series. The identification of vertebrae as the true sacrals is based upon their position adjacent to the ischial peduncle of the ilium, and the presence of large sacral ribs that articulate via large facets mostly on the centrum. The true sacrals also retain large transverse processes dorsal to their sacral ribs.

Eoraptor has at least three sacral vertebrae (Sereno et al., 1993; pers. obs.), the most anterior of which (vertebra 25) is taken from the dorsal series. The primordial sacrals are numbers 26 and 27 in the series. Vertebra 28 is partially obscured in the cast available for study, and I cannot be certain at this time if it had an iliac articulation. The more intact right ilium of the holotype has a long postacetabular process, and there is space enough along the medial margin of the brevis shelf for a fourth sacral vertebra. I suspect, but cannot confirm, that vertebra 28 in *Eoraptor* is a caudosacral, and that the sacral formula in this taxon is dS1 + S1 + S2 + cS1 (Fig. 50E). The incorporation of vertebra 28 into the sacrum is coded as missing data for *Eoraptor*.

All other theropods known from adequate material have at least five sacral vertebrae. *Coelophysis* and *Syntarsus rhodesiensis* each have 10 cervicals, 13 dorsals, and five sacrals, for a count of 28 precaudal vertebrae. *Dilophosaurus* has nine or 10 cervicals, either 14 or 13 dorsals respectively, and five sacrals (contra Welles, 1984), for a total of 28 pre-caudals. *Carnotaurus*, an abelisaurid with at least six sacrals, has 10 cervicals, 12 dorsals, and six sacrals, for a total of 28 precaudals (Fig. 50D). The tetanuran *Allosaurus* has nine cervicals, 14 dorsals, and five sacrals for again a total of 28 pre-caudal vertebrae (Fig. 50C). The same precaudal count is present (with only a difference in the number of cervical versus dorsal vertebrae) in other basal tetanurans, such as *Sinraptor dongi* (Currie and Zhao, 1993), *Monolophosaurus jiangi* (Zhao and Currie, 1993), and even in the relatively basal coelurosaur *Tyrannosaurus rex* (Osborn, 1906; Brochu, 2002).

Several morphological details are evidence against the sacral homology hypothesized by Madsen (1976), Molnar et al. (1990), Sereno (1999a), and Tykoski and Rowe (2004). The 25th vertebra in many theropods bears a sacral rib, but it is usually positioned on the neural arch rather than the centrum body (but has centrum contact in *Allosaurus* [Madsen, 1976]). This rib is almost always smaller than the two succeeding sacral ribs, which are positioned on the centrum as in Reptilia ancestrally (Romer, 1956). The 25th vertebra also retains a 'dorsal-like' morphology. The 27th vertebra exhibits features not normally associated with caudal vertebrae, such as separate transverse processes and sacral ribs, and incipient diapophyseal laminae dorsal to the sacral ribs. The contact between vertebrae 25 and 26 is also adjacent to the acetabulum or even the pubic peduncle of the ilium in some taxa, a point far anterior to the juncture of the true sacrals in archosaurs ancestrally.

It is more likely that vertebrae 26 and 27 are the true sacrals in Saurischia. I hypothesize the three-vertebra sacrum of some prosauropods was formed by the incorporation of a caudal vertebra (Fig. 50B), with some taxa shifting assimilation of the third sacral from the caudal to the dorsal series. *Eoraptor* bears three or possibly four sacral vertebrae, with one clearly from the dorsal series and the possible fourth from the caudal series (Fig. 50E). Other basal theropods known from adequate material have at least five sacrals, with one caudosacral and a minimum two dorsosacrals added to the sacral series (Fig. 50D, F).

The obvious questions that arise are whether there is a phylogenetic signal to the incorporation of the vertebrae into the sacrum, and what is the sequence of 'sacralization'

of the affected vertebrae? The answers to these questions are determined by fragmenting the formation of the theropod sacrum into several discrete characters. The incorporation of vertebrae 23, 24, 25, and 28 into the sacrum are treated as separate characters. The evolution of the theropod sacrum should be revealed as a series of character transformations mapped on the resulting hypotheses of phylogeny. This is an *a posteriori* approach to determine the evolution of the theropod sacrum, and should provide robust support for the resulting hypothesis of sacral formation in Theropoda.

The 23rd vertebra is usually the last pre-sacral vertebra in theropods. It often lies between the preacetabular processes of the ilia, but does not contact the ilial walls. In some taxa this vertebra is incorporated into the sacral series, determined by contact between the diapophyses and ilia, and by co-ossification of the centrum to the succeeding sacral vertebra (vertebra 24-dorsosacral 2). This character is present in *Elaphrosaurus*, *Ceratosaurus*, and *Carnotaurus*. It must be noted that the exact pre-caudal vertebral count is estimated for *Elaphrosaurus* and *Ceratosaurus* because vertebrae are missing in both taxa. Both taxa also have six vertebrae in the sacrum. Otherwise they resemble the 'normal' theropod condition in having primordial sacrals (normally vertebrae 26 and 27) positioned adjacent to the ischial peduncles of the ilia, and a single sacral posterior to these (normally vertebra 28) (Fig. 51A). The three dorsosacrals anterior to the primordials are therefore interpreted to be vertebrae 23-25, and character 169 is scored as present in both taxa.

The exact homology of the sacrals in the abelisaurid *Carnotaurus* is debatable. There are 28 precaudal vertebrae, the last six of which are fused to one another as a

synsacrum. In this regard it closely resembles *Elaphrosaurus* and *Ceratosaurus*. Bonaparte et al., (1990) included the 22nd vertebra in the sacral series because of a small amount of co-ossification between its postzygapophyses and the prezygapophyses of vertebra 23. However, there appears to be only incidental contact between one of the transverse processes and the ilium in this vertebra, and there is a clear separation between the centra of this and the successive vertebra. It is not counted as a sacral vertebra for the purpose of this study.

The distribution and relative size of the sacral ribs and transverse processes is unusual in *Carnotaurus*. Four of the sacral vertebrae bear sacral ribs, and the largest ribs are borne on vertebrae 24 and 25 instead of the assumed primordial sacrals (vertebrae 26 and 27) (Figs. 50D, 51B). If the lateral view illustration of the sacrum provided by Bonaparte et al., (1990) is accurate, then the morphology of the transverse processes of the posterior sacrals is also abnormal. It is assumed that the true sacrals of this taxon are vertebrae 26 and 27, and I agree with Carrano et al. (2002) that there is one caudosacral and three dorsosacrals in the sacrum.

145. Vertebra 24 part of dorsal vertebral series (0), or incorporated into sacral series (as dorsosacral 2) (1).

The explanations of sacral homology are described above. The 24th vertebra in the axial column is the first in the sacral series in those theropods with a five-vertebra sacrum. This includes all theropods more derived than *Eoraptor* and *Herrerasaurus* (if the latter is a theropod). It was originally claimed that four vertebrae comprised the

sacrum of *Dilophosaurus*, and the 24th vertebra was identified as the last of the dorsal series in the taxon (Welles, 1984). Examination of the type specimen (UCMP 37302) revealed the vertebra in question is almost completely reconstructed in plaster, including the neural arch and transverse processes (Fig. 52A, C). The anterior half of the type ilium is also missing and is reconstructed in plaster, so there is no way to examine it for a contact scar from the diapophysis of vertebra 24. It is impossible to make an accurate statement about whether or not vertebra 24 had any contact with the ilium based upon the type specimen.

The *Dilophosaurus* individual from the Gold Spring area of Arizona in the collections of the Texas Memorial Museum Vertebrate Paleontology Laboratory (TMM 43646) preserves the disarticulated sacral series in association with both ilia and hindlimbs. The sacral centra have not been identified with certainty, but at least four of the sacral neural arches are present (TMM 43646-68, -70, -71), and a fifth specimen (TMM 43646-69) may be the neural arch of caudosacral 1. The left ilium (TMM 43646-60 is the better preserved of the two, and its medial surface bears scars at the contact points of the sacral ribs and transverse processes (Fig. 52B). The relative size, shape, and position of these scars are almost identical to those on the left ilium of TMM 43688-1, a sub-adult *"Syntarsus" kayentakatae*. The second sacral rib of TMM 43688-1 fits into a sharp scar directly dorsal to the ischial peduncle of the ilium, so the relationship of sacral ribs and transverse processes can be unambiguously aligned with the other sacral contact scars on the medial surface of the ilium. The anterior end of the ilium is missing in TMM 43688-1, so the contact scar for the second dorsosacral is indeterminate. The shape and

position of the sacral ribs and their contacts with the ilia in TMM 43688-1 are also consistent with articulated specimens of the Shake-N-Bake taxon (MCZ 9442). Comparisons between these taxa show five vertebrae comprised the sacrum in *Dilophosaurus* (Fig. 52C), and that the morphology and relative size of the sacrum in *Dilophosaurus* closely resembles the sacrum of other coelophysoids (Figs. 50F, 52D).

146. Vertebra 25 part of dorsal vertebral series (0), or incorporated into sacral series (as dorsosacral 1) (1).

147. Vertebra 28 part of caudal vertebral series (0), or incorporated into sacral series (as caudosacral 1) (1).

148. Ventral margin of sacral series relatively straight (0), or exhibits strong dorsal-ward arching (1) (Holtz, 1994, 1998; Sereno, 1999a).

149. Diameter of mid-sacral centra approximately the same (0), or substantially smaller (1) than posterior dorsals and anterior caudals (Holtz, 1994, 1998).

150. Sacral centra remain separate or exhibit limited co-ossification (0), or exhibit full fusion to one another so sutures nearly indiscernible (1) by adulthood (modification of Rowe, 1989; Rowe and Gauthier, 1990).

The sacral centra are variably intergrown or co-ossified in many archosaur taxa, and this feature is highly dependent upon the ontogenetic stage of a given individual. Adult specimens of many non-avian theropods exhibit minor or partial co-ossification in some or all of the sacral centra. In most of these taxa ossification or intergrowth occurs on the surface of the intervertebral contacts, so the anterior and posterior rims individual centra remain easily discernable, even in large individuals that are assumed to be adults (Madsen, 1976; Brochu, 2002). The variability in degree and ontogeny of sacral fusion in theropods was recently used as justification for ignoring this character in phylogenetic analyses of basal theropod relationships (Rauhut, 2003).

The degree and style of sacral fusion are highly derived in coelophysoids, *Elaphrosaurus*, *Ceratosaurus*, and abelisauroids. The resulting morphology represents a potentially informative phylogenetic character, contrary to recent assertions (Rauhut, 2003) and should be included in subsequent analyses. The sacral centra of the aforementioned taxa are so thoroughly fused by adulthood that the intervertebral contacts are discernable only as gentle swellings along the body of the resulting synsacrum (Figs. 51, 52D, 53C, D). Faint suture lines are sometimes present between the fused sacral centra in small individuals of *Coelophysis* (AMNH 2722, TMM 45559-3), and the Shake-N-Bake taxon (MCZ 9442) (Fig. 53A, B). The suture lines are far less noticeable or absent between the fused centra in larger specimens of the Shake-N-Bake taxon (TMM 43689-11). Clearly, the sacral centra fuse early in the ontogeny of coelophysoids relative to other theropod taxa. This is observable in specimens such as TMM 43688-1, a sub-adult *"Syntarsus" kayentakatae* with completely obliterated intercentral sutures in the

sacrum (Fig. 53C, D). Similar extensive sacral fusion was described for *Ceratosaurus*, *Elaphrosaurus*, *Carnotaurus*, and *Masiakasaurus* (Gilmore, 1920; Janensch, 1925; Bonaparte et al., 1990; Carrano et al., 2002).

The results of the ontogenetic analyses (see Chapter 1) show that most of the known specimens of *Dilophosaurus* come from immature individuals, the exception being UCMP 77270. A partial synsacrum is preserved with the latter specimen, including a number of sacral ribs and transverse processes. The sacral centra of this specimen were eroded away prior to collection, and were not recovered. It is currently impossible to determine if extensive cossification between the sacral centra was present in *Dilophosaurus*, because the other known individuals are not ontogenetically developed enough to assess the character. The same is likely true of *Liliensternus*, another taxon known from individuals that exhibit features consistent with at most a sub-adult stage of development. Two co-ossified sacral vertebrae (MB 2175.2.26) are known that were assigned to the larger of at least two individuals recovered from the type locality. The more anterior vertebra is probably one of the true sacrals, but it is difficult to determine if the more posterior vertebra is the second sacral or the first caudosacral. The two centra are co-ossified, but the suture between their articular surfaces is clearly visible. I code the character as missing data in *Liliensternus* until more mature specimens are discovered.

151. Sacral neural arch elements (transverse processes, arches, neural spines) and sacral ribs of adjacent vertebrae remain separate (0), or fuse to one another by adulthood (1) (Rowe, 1989; Rowe and Gauthier, 1990).

This character was previously combined with the fusion of the sacral centra and treated as a single character state. However, it possibile these two sets of features could vary independently, and that one is not a prerequisite or direct outcome of the other. For example, the neural arch elements are fused to one another in *Herrerasaurus*, but the sacral centra are not fully fused.

This character is another that may be expressed only in later stages of ontogeny. As such, it cannot be critically evaluated in taxa not represented by specimens of sufficient ontogenetic development. This character is present in at least one specimen of *Dilophosaurus* (UCMP 77270) and is therefore coded as present in the taxon. There are also some taxa for which neural arch fusion is present, but the specimens do not preserve the sacral centra themselves, or visa versa (e.g., *Dilophosaurus* UCMP 77270, *"Syntarsus" kayentakatae* TMM 43688-1). If sacral centrum fusion and sacral neural arch fusion were made a single character it would have to be scored as unknown for these taxa because half of the sacral anatomy encompassed by such a mulitple component character description is unknown in each taxon. This results in a loss of phylogenetic data in the analysis, even though morphologically informative anatomy is present in each taxon.

A partial synsacrum (FMNH PR 2142) of the abelisauroid *Masiakasaurus* was described and figured by Carrano et al. (2002). Errors were probably made in that

description with regard to the identification of several structures in the synsacrum of *Masiakasaurus*. The 'transverse processes' sensu Carrano et al. (2002) are the sacral ribs, the 'spine table' is the remnants of the co-ossified transverse processes, and the 'central strut' is the homologue to the paradiapophyseal lamina (sensu Wilson, 1999) present in the dorsal vertebral neural arches of saurischians (Carrano et al., 2002:fig. 9A-C) (Fig. 54A). The sacral arrangement and morphology in FMNH PR 2142 is consistent (albeit derived) with that present in coelophysoids and other basal theropods, such as the Shake-N-Bake taxon (Fig 54B). It appears that the sequence of sacral vertebrae as labeled in figure 9A of Carrano et al. (2002) is reversed, but is correct in their figures 9B and 9C. I identify the vertebrae in this specimen as either dS1 + S1 + S2, or dS2 + dS1 + S1, given the relative size and position of sacral ribs (Fig. 54C). The ribs, neural arches, neural spines, and proximal bases of the transverse processes are also fused in this specimen.

152. Sacral transverse process of at least mid-sacrals remain separate (0), or coalesce to form nearly continuous horizontal sheet in dorsal view (1) by adulthood (Rauhut, 2003).

The transverse processes of coelophysoids, *Elaphrosaurus*, and *Ceratosaurus* not only fuse to the adjacent transverse processes proximally along the neural arch, but also distally (laterally). The processes expand anteroposteriorly toward the distal ends, contacting one another before meeting the medial surface of the ilium. The transverse processes of the second dorsosacral (dS2) do not contact the processes of the first

dorsosacral, so this character applies only to the first dorsosacral through the first caudosacral vertebrae.

The broad proximal and distal contacts and subsequent coalescence of the sacral transverse processes create an extensive horizontal lamina of bone that roofs the sacral ribs, centra, and the brevis shelves of the ilia (Fig. 55A, B). The lamina is broken in coelophysoids and *Elaphrosaurus* (Janensch, 1925) by only one or two small fenestrations or foramina centered between transverse processes. It is difficult to tell in illustrations of *Ceratosaurus*, but it appears that there are foramina in the horizontal lamina between nearly all the transverse processes in the sacrum (Fig. 51A) (Gilmore, 1920). The sacral transverse processes in *Carnotaurus* do not appear to be in contact with one another distally, and therefore do not form an extensive lamina dorsal to the sacral ribs (Bonaparte et al., 1990). The partial sacrum of *Masiakasaurus* (FMNH PR 2142) preserves only the proximal edges of what appears to be coalesced transverse processes, so it is not known if they were also fused distally (Fig. 54A, C).

The sacral transverse processes were often misidentified by previous authors. In some cases the structures were identified as sacral ribs simply because they contact the ilium (Colbert, 1989; Rauhut, 2003). These structures are not homologous to sacral ribs. Sacral ribs are ventral to the transverse processes on the primordial sacrals (S1, S2), and often on the first dorsosacral (dS1). The ilial contacts between the second dorsosacral (dS2) and the first caudosacral (cS1) of most non-avian theropods are made via transverse processes, albeit highly modified on the first caudosacral. The fused sacral

transverse processes of *Masiakasaurus* were incorrectly identified as a continuous spine table (Fig. 54A) (Carrano et al., 2002).

153. Sacral ribs and transverse processes remain separate (0), or fuse to ilia (1) in adults (Rowe 1989; Rowe and Gauthier, 1990).

Fusion between the sacral ribs and transverse processes and the ilia is present in all adequately preserved coelophysoid taxa known from adult specimens (see Chapter 1 and Table 3). There is no sign of fusion between these elements in a sub-adult *"Syntarsus" kayentakatae* (TMM 43688-1) with fully fused sacral centra and ribs, as well as co-ossified pelvic bones. A number of Shake-N-Bake specimens are isolated pelves or sacra, with no sign of breaks along the sacro-iliac contacts. A fused Shake-N-Bake specimen (MCZ 9442) retains only faint lines of suture visible between the broad distal ends of the sacral ribs and the surface of the ilium (Fig. 56). Among specimens of *Dilophosaurus*, only the adult specimen UCMP 77270 exhibits this character (see Chapter 1). Fusion between these elements is also present in *Elaphrosaurus* and *Ceratosaurus*. There is no explicit mention of sacrum-ilium fusion in the abelisaurid *Carnotaurus*, so the character is coded as missing data for the taxon. The same is done for *Masiakasaurus* because the distal ends of the sacral ribs and transverse processes are missing from the only sacral specimen known (FMNH PR 2142). A well-preserved, disarticulated left ilium is known for the abelisaurid *Majungatholus* (UA 8678), but the individual from which it came was described was said to show signs of relative immaturity in the skeleton (Sampson et al., 1998).

This character was not included in the analysis of Carrano et al. (2002), and it was dismissed by Rauhut (2003) as being too variable ontogenetically. This ignored the fact that formation of a synsacrum does not occur in adults of the proximal outgroups to Theropoda, nor is there evidence that it occurred in basal tetanurans. Indeed, synsacra do not appear among tetanurans until the appearance of some coelurosaurian clades. The synsacrum in coelophysoids, *Elaphrosaurus*, and *Ceratosaurus* has the potential to be phylogenetically informative, and as such it should be included in any analysis of basal Theropoda. The character can only be demonstrated to be non-informative by *a posteriori* examination of its distribution in a hypothesis of relationship.

154. Ventral surface of caudal centra smooth or bear shallow longitudinal groove (0), or bear narrow, sharp longitudinal groove (1) (Rowe and Gauthier, 1990).

This character is somewhat vague in its wording, but the feature described is undoubtedly present in a number of coelophysoid specimens. Many theropods have median sulci along the ventral surface of the caudal vertebrae. Many of the caudals in coelophysoids and *Ceratosaurus* (Gilmore, 1920) have a very distinct ventral groove (Fig. 57A-C). The groove in these forms is much more pronounced than the sulcus often seen on caudal vertebrae. The actual distribution of these sharply grooved caudals along the axial column is not clear because a complete and intact caudal series is not known for most of them. Suffice it to say for now that at least some of the caudals in these taxa bear a unique ventral groove morphology.

155. Distal ends of transverse processes of anterior caudal vertebrae not expanded (0), or anteroposteriorly expanded (1) (Coria and Salgado, 1998).

156. Hyposphene-hypantrum articulations absent (0), or present (1) on anterior and mid-caudal vertebral arches (Coria et al., 2002).

157. Neural spines of mid-caudal vertebrae rod-like and posteriorly inclined (0), or tall, rod-like, and vertically directed (1) (Rauhut, 2003).

158. Neural arch elements (transverse processes, neural spines) not abruptly reduced in caudal series (0), or reduced in distal caudal vertebrae (1), or reduced in mid-caudal vertebrae (2) (modified from Gauthier, 1986). (O)

This and the following character are rewordings of Gauthier's (1986) single character describing the position of the transition point in the tail of theropod dinosaurs. As originally envisioned, the transition point is where the caudal neural arch processes (transverse processes and neural spine) exhibit dramatic reduction in size, and the tail distal to this point is stiffened.

Interpretations of what constitutes the transition point can differ between workers. Gauthier (1986) described the transition point in the theropod tail in reference modification of three separate vertebral components. These were the reduction of the neural arches and transverse processes, elongation of the caudal prezygapophyses, and reduction of the haemal arches. He pointed out that these three features did not occur at

the same caudal vertebra, but rather over the span of a few vertebrae, and that the transition point referred collectively to the short span of the tail that encompassed all of these changes. Therefore, the development and location of the individual structural components that result in a caudal transition point are scored here, rather than the presence and position of the transition point itself. This also allows the characters to be scored from even an individual vertebra from corresponding parts of the caudal series. Determining the position of the transition point requires a relatively complete caudal series, which greatly reduces the number of taxa for which the character can be evaluated.

Marked reduction of neural arch elements is present in the distal caudal vertebrae of *Herrerasaurus*, *Dilophosaurus*, *Coelophysis*, *Syntarsus rhodesiensis*, the Shake-N-Bake taxon, *Masiakasaurus*, *Allosaurus*, and *Ornitholestes*. The distal caudals are not known in *Eoraptor*, *Segisaurus*, *"Syntarsus" kayentakatae*, *Liliensternus*, *Ceratosaurus*, *Elaphrosaurus*, abelisaurids, *Torvosaurus*, spinosaurids, "*Poekilopleuron*" *valedunensis*, and *Eustreptospondylus*, and hence cannot be evaluated. However, the distal caudals have strongly reduced neural arch components in virtually all tetanurans for which distal caudals are known.

159. Distal caudal vertebral zygapophyses with <25% overlap (0), or 25%<50% overlap (1), or ≥50% overlap (2) of preceding centrum (modified from Gauthier, 1986; Holtz, 1998; Rauhut, 2003). (O)

This anatomical feature was first used by Gauthier (1986) as one of the suite of novelties that collectively marked a transition point in the tail of theropods. There was

originally no quantitative percentage of prezygapophyseal overlap given to indicate the derived condition. The prezygapophyses of the distal caudal vertebrae were recognized as derived because they were "elongate, pointed anteriorly, and clasp the elongate, blocklike postzygapophysial moiety" (Gauthier, 1986:19).

One-half centrum length overlap was used by Holtz (1998) as the arbiter between primitive and derived states, with less than one-half centrum length being the primitive condition. Prezygapophyses that overlapped more than 25% the preceding vertebra was the derived condition of Rauhut (2003). The use of 50% as the cut-off for the derived prezygapophyseal condition relegated many theropods to being coded the same as non-theropod taxa such as sauropodomorphs and ornithischians, with considerable loss of potential phylogenetic signal. Likewise, it should be recognized that there is a distinct difference between the relative size of the distal caudal prezygapophyses of basal theropods and more derived taxa. Each condition is treated as a separate character state here.

The prezygapophyses on the distal caudals overlaps 25% or more of the preceding centrum in *Herrerasaurus*, and almost all other theropods for which distal caudal vertebrae are known. It was reported that the condition is absent in *Coelophysis* (Rauhut, 2003), and I have not been able to confirm or refute the claim at this time. The absence of this feature is doubtfully coded for the taxon. This character state was also assigned to *Dilophosaurus* by Rauhut (2003). A well preserved, articulated series of mid- to distal caudal vertebrae is now known for *Dilophosaurus* (TMM 43646-140). The prezygapophyses on the distal caudals are more than 25% the length of the preceding

centrum, and may be almost 50% in some of the vertebrae (Fig. 58). The prezygapophyses of the distal caudal vertebrae unequivocally overlap half or more of the preceding centrum in *Herrerasaurus*, *Allosaurus*, and *Ornitholestes* in this study. The feature is also present in almost all tetanurans for which the distal caudal vertebrae are known. The status of this character is not known in the other taxa in this analysis.

160. Mid and distal haemal arches (chevrons) rod-like or slightly expanded distally (0), or L-shaped (1) in lateral view (Carrano et al., 2002).

161. Anterior processes on proximal end of haemal arches (chevrons) absent (0), or small tubercules (1), or large and projecting (2) (Carrano et al., 2002). (UO)

162. Furcula (=median fusion of clavicles) absent (0), or present (1) (Holtz, 1994, 1998).

Furculae were once considered a strictly avian or avialian feature within Theropoda. Discoveries over the past twenty years have forced a basal-ward march for this character down the theropod lineage. Over this time the furcula was successively considered diagnostic of Maniraptora (Bryant and Russell, 1993), Avetheropoda (Holtz, 1998), and eventually Tetanurae (Makovicky and Currie, 1998). The nearly simultaneous discoveries of furculae in the coelophysoids *"Syntarsus" kayentakatae* (Tykoski, 1998), *Coelophysis* (Downs, 2000), *Segisaurus* (Senter and Hutchinson, 2001), and *Syntarsus rhodesiensis* (Tykoski et al., 2002) unequivocally demonstrated this element was present in non-tetauran taxa.

No furcula is known from specimens of *Dilophosaurus*, *Liliensternus*, *Ceratosaurus*, or any abelisaurid. The absence of this element in known specimens does not necessarily indicate actual absence of the character in a taxon (Makovicky and Currie, 1998). Instead, its absence may represent negative evidence. Most of the taxa for which the furcula is not known are represented by incomplete material, or the quality of preservation in the specimen leaves open the possibility that the element was present in life but was not preserved. For example, prior to 2002 the most basal tetanuran for which a furcula was known was *Allosaurus* (Chure and Madsen, 1996). New spinosaurid specimens were then found that possessed the rarely preserved furcula, illustrating the importance of preservational bias in the distribution of this character among theropods (Lipkin and Sereno, 2002). The presence of a furcula may also go unnoticed, or the element may be misidentified for years, as the case was with specimens of tyrannosaurids, *Allosaurus*, *Syntarsus rhodesiensis*, and *"Syntarsus" kayentakatae* (Chure and Madsen, 1996; Makovicky and Currie, 1998; Tykoski et al., 2002).

I leave this character coded as missing data in most of the taxa for which the furcula is not currently represented. It is coded as absent in *Plateosaurus* and *Eoraptor*. *Plateosaurus* is known from multiple specimens, many of which are well preserved and nearly complete. Paired, rodlike clavicles are known for *Plateosaurus* (Galton, 2001a) but no furcula was reported in any of these specimens. The type specimen of *Eoraptor lunensis* is a skeleton that includes a nearly complete right pectoral girdle, and parts of the left. There is no sign of clavicular elements in the cast of the *Eoraptor* type specimen available to me (TMM 43451-2), so the derived state is scored as absent in *Eoraptor*.

Tykoski et al. (2002) claimed that a strict interpretation of the distribution of the furcula among theropods would result in the interpretation that the element arose twice in the history of Theropoda. This statement was not supported by an actual analysis. Instead, it was made by visual evaluation of the distribution of furculae on two cladograms with conflicting hypotheses of theropod phylogeny. The present study is the first in which the furcula is scored as present in *Coelophysis*, *"Syntarsus" kayentakatae*, *Syntarsus rhodesiensis*, *Segisaurus*, and the spinosaurid *Suchomimus*. Based upon the preferred tree generated by this analysis (see Figures 108A-F below) the furcula arose once in the evolutionary history of Theropoda, in the most recent common ancestor of *Coelophysis* and *Allosaurus*.

163. Scapular blade broad and relatively short, ratio of maximum length/minimum breadth <10 (0), or blade narrow and long, ratio of maximum length/minimum breadth ≥10 (1) (modified from Gauthier, 1986; Holtz, 1994; Rauhut, 2003).

In this work, all descriptions and references to the scapula and coracoid are made with the two elements arranged in a vertical orientation, with the glenoid fossa on the posterior edge of the combined scapulocoracoid, and the acromion process located along the anterior margin of the scapula. The distal end of the scapular blade is directed dorsally, and the coracoid meets the scapula along the ventral margin of the latter. This is the orientation of the scapula and coracoid used by theropod workers for decades. In contrast, Rauhut (2003) described characters of the pectoral girdle with the scapula and coracoid with the long axis of the combined elements oriented horizontally. In other

words, the glenoid fossa faced ventrally, the acromion process dorsally, the distal tip of the scapular blade posteriorly, and the coracoid was positioned anterior to the scapula. The differences between these orientations should be kept in mind when referencing both works.

The scapular blade is measured here from the dorsal edge of the acromion process to the distal tip of the scapula (Fig. 59A). The exception is in those taxa that lack an abrupt transition from the acromion process to the scapular blade. The measurement is arbitrarily taken from the most distal inflection point proximal to the greatest constriction of the scapular blade to the distal tip of the blade in such cases (Fig. 59B). These differ from the reference points used by Rauhut (2003), who compared the minimum width of the scapular blade to the entire length of the scapula, from the coracoid contact to the distal tip. This character was originally meant (sensu Gauthier, 1986) to emphasize the change from the relatively broad scapulae present in Theropoda ancestrally to the long, narrow, strap-like scapula present in many tetanuran taxa. The length and narrowness of the scapular blade may be independent of the size of the scapula proximal to the acromion process. Hence, the proximal part of the scapula is excluded from measurements here.

A strap-like scapular blade was once considered a tetanuran synapomorphy (Gauthier, 1986). The derived state for this character is unambiguously present in only one tetanuran in my analysis, *Allosaurus*. The scapula is unknown in *Ornitholestes*, *Eustreptospondylus*, "*Poekilopleuron*" *valedunensis*, and *Torvosaurus*. The scapula is present in *Baryonyx* and *Suchomimus*, but does not exhibit the derived condition. The

character would be uninformative in the present analysis if not for the fact that the derived state is present in *Segisaurus*.

The scapula of the type and only known specimen of *Segisaurus* is broken into two pieces on separate blocks, but the pieces can be arranged into the correct anatomical position. The acromion process is visible so a measurement can be taken on the specimen. The scapula is very narrow at its constriction distal to the acromion process, and the blade is more than ten times longer than its width at its narrowest constriction (Fig. 59C). This is very different than the condition present among other coelophysoids, the group to which *Segisaurus* is usually referred.

164. Distal end of scapular blade markedly expanded (0), or not expanded (1) (Currie and Zhao, 1993; Carrano et al., 2002).

This character is taken from Gauthier (1986) who noted a strap-like scapula present in some tetanuran theropods. The distribution of taxa that lack a distal expansion of the scapular blade is now known to be greater than previously thought. The presence or absence of a distal expansion of the blade is not dependent upon the rest of the scapula being exceptionally narrow for its length. Therefore the character is treated separately here.

The distal end of the scapula is markedly broader anteroposteriorly than the more proximal parts of the scapular blade in archosaurs ancestrally. The primitive morphology is retained in ornithischians, sauropodomorphs, *Eoraptor*, and coelophysoids (Fig. 60A, B). The morphology of the distal scapular blade is not known or not published for

Elaphrosaurus, *Masiakasaurus*, *Ilokelesia*, *Abelisaurus*, *Majungatholus*, *Torvosaurus*, *Irritator*, "*Poekilopleuron*" *valedunensis*, and *Ornitholestes*. The distal scapular blade is not expanded to an appreciable degree in *Herrerasaurus*, *Ceratosaurus*, *Aucasaurus*, *Carnotaurus*, probably *Baryonyx*, *Eustreptospondylus*, and *Allosaurus* (Fig. 60C, D). The condition is also present in virtually all theropods more derived than *Allosaurus* known from adequate material.

The condition of the distal scapula is uncertain for *Baryonyx* because the distalmost extremity of the scapular blade is missing. The blade shows no sign of expanding by the point of the break, but it is remotely possible that it was present in the missing part of the scapular blade. An outline of the scapula of *Suchomimus* was provided as part of a skeletal reconstruction of the taxon, but was not figured more clearly than that. The blade appears to be expanded at its distal end, and is in general broader than the corresponding element in *Baryonyx*. An expanded distal end of the scapular blade is coded as present in *Suchomimus*, pending a more thorough description.

165. Posterior margin of scapular blade curves over full length (0), or nearly straight over most of length, curves posteriorly only at distal tip (1).

The anterior and posterior margins of the scapular blade are both concave in lateral view in dinosaurs ancestrally (Fig. 61A). The posterior margin of the scapular blade is derived in many coelophysoids in that it is virtually straight for most of its length distal to the glenoid fossa (Fig. 61B-D). The posterior margin curves posteriorly only

near the distal tip of the blade. The anterior margin of the scapula is strongly curved, so that most of the distal expansion of the scapular blade is directed anteriorly.

This character is present in specimens of *Coelophysis* (AMNH 7223, 7224; contra Colbert, 1989) (Fig. 61B), *Segisaurus* (Fig. 59C), *Syntarsus rhodesiensis* (Fig. 61C), *"Syntarsus" kayentakatae* (MNA V2623) (Fig. 60A), *Gojirasaurus quayi* (Fig. 61D), and at least one specimen of *Dilophosaurus* (UCMP 77270). The scapula of *Segisaurus* lacks the posterior curvature of the blade near the distal tip, so the entire posterior margin of the scapula distal to the glenoid fossa is straight. The posterior margin of the scapula is also straight in the abelisaurids *Aucasaurus* and *Carnotaurus*, which also completely lack a distal expansion to the scapular blade.

Dilophosaurus is a problematic taxon with regard to this character. Both scapulae are present in the type (UCMP 37302), and at least one scapulocoracoid is present in UCMP 77270. The posterior margin of the left scapula in both UCMP 37302 and UCMP 77270 exhibits the derived condition for this character (contra Welles, 1984), and in all other respects resembles the same elements in smaller taxa such as *Coelophysis* and *Syntarsus rhodesiensis*. The right scapula of the type retains the morphology of the primitive condition, with a posterior margin that describes a gentle arc (Fig. 60B).

166. Anterodorsal border of acromion process of scapula protrudes conspicuously (0), or has smooth, continuous, high-angle transition to scapular blade (1) (modified from Rauhut, 2003).

The acromion process of the scapula and the scapular blade are clearly set off from one another in most basal members of dinosaur clades. Within Theropoda, the condition persists in *Eoraptor*, many coelophysoids, and non-coelurosaurian tetanurans (Fig. 61A-D, 63D). The transition from the acromion process to the scapular blade is noticably continuous in *Ceratosaurus*, *Carnotaurus*, and the coelophysoids *Segisaurus* and *"Syntarsus" kayentakatae*. The anterior margin of the scapula describes an arc from the scapula-coracoid contact to the base of the scapular blade in *Ceratosaurus* (Fig. 62A). The anterodorsal margin of the acromion process is not curved in *Carnotaurus*, *"Syntarsus" kayentakatae*, or *Segisaurus*. Instead, the margin of the acromion process is more linear and rises posterodorsally at a high angle from the acromion to merge with the scapular blade (Fig. 62B-D). This is especially the case with *Segisaurus*, in which the acromion process is nearly indiscernible from the scapula-coracoid junction to the scapular blade (Fig. 59C, 62D).

This character cannot be scored for *Dilophosaurus*. The acromion process is not fully preserved in any specimen recovered to date. The description of the acromion of the type scapula (UCMP 37302; Welles, 1984) was based upon a plaster reconstruction (Fig. 60B). The anterior margin of the acromion is also missing in the scapula of the referred specimen UCMP 77270. It is noted here that the squared off anterior edge of the scapular blade's distal end, a character used to diagnose *Dilophosaurus* (Rauhut, 2003), is present only on the left scapula of UCMP 37302. It is not present on the right scapula of the same individual, or on the scapula of the referred specimen UCMP 77270. This morphological feature should not be used as a diagnostic apomorphy for the taxon until it

is determined whether it is more widely distributed or it is an abnormality unique to this individual.

167. Anterior margin of scapulocoracoid at scapula-coracoid contact notched (0), or continuous and uninterrupted (1) in adults (Holtz, 1998).

The scapula-coracoid juncture is marked in most dinosaurs by a weak notch or indentation along the anterior margin of the scapulocoracoid complex (Fig. 61A, B). This condition is especially clear in sauropodomorphs, *Eoraptor*, and those basal tetanuran theropods for which the pectoral girdle is known, including *Allosaurus*.

The anterior margin of the scapulocoracoid has an arced profile that is uninterrupted by a notch in *Herrerasaurus*, *Segisaurus*, *"Syntarsus" kayentakatae* (Fig. 62C), *Ceratosaurus* (Fig. 62A), and *Carnotaurus* (Fig. 62B). This apomorphy is best viewed in material representing adult or near-adult individuals, and it is possible that is is only expressed in adult individuals. This character cannot be evaluated most of the theropod taxa in this analysis because if incompleteness or lack of preservation of this part of the pectoral girdle. This is the case with the coelophysoids *Dilophosaurus*, *Liliensternus*, and *Syntarsus rhodesiensis*. It was stated that the area in question was not well preserved in specimens of *S. rhodesiensis* (Fig. 61C), but the scapulocoracoid margin was reconstructed with a notch at the scapula-coracoid contact anyway (Raath, 1977). A large number of *Coelophysis* scapulocoracoids are undoubtedly present in the collections from Ghost Ranch. The material is insufficiently described and figured at this time to accurately score this character in *Coelophysis*. The anterior margin of the

scapulocaoracoid appears to have a faint notch at the scapula-coracoid contact in at least one *Coelophysis* specimen in the collection of the Cleveland Museum of Natural History (Fig. 61B). This character is coded as missing data for *Coelophysis*.

168. Posteroventral process of coracoid not expanded beyond glenoid fossa (0), or expanded beyond margin of glenoid fossa (1) (Sereno et al., 1996).

The coracoid is bluntly rounded off and projects little or not at all beyond the ventral margin of the glenoid fossa in sauropodomorphs, *Eoraptor*, coelophysoids, and *Ceratosaurus* (Fig. 59, 60A, C, 61B, C, 62A, C, D, 63A). The coracoid is posteroventrally expanded to form a pointed process that projects well beyond the glenoid fossa in *Elaphrosaurus*, abelisaurids and tetanurans (Fig. 62B-D). The posteroventral processes present on coracoids referred to *Elaphrosaurus* (Janensch, 1929) and those of basal tetanurans are separated from the glenoid fossa by a concavity in the coracoid margin. This gives the posteroventral process a hook-like profile in lateral and medial views (Figs. 63C, D). The posteroventral process is even more greatly enlarged in *Carnotaurus*, projecting far beyond the glenoid, contributing to a very large coracoid relative to the breadth of the scapula (Fig. 63B). There is no concavity in the coracoid margin between the glenoid fossa and the posteroventral process in *Carnotaurus*, so it lacks the hook-like profile of *Elaphrosaurus* and basal tetanurans.

169. Humerus length ≥1/3 (0), or <1/3 (1) femur length (Novas, 1993).

170. Humerus proximal head flattened (0), or rounded, bulbous, subspherical (1) (Holtz, 1998; Rauhut, 2000).

171. Humerus with anteroposterior sigmoid curvature (0), or is straight (1) in lateral view (Sereno, 1999a; Rauhut, 2003).

172. Humerus shaft torsion absent (0), or present (1) (Holtz, 1998).

Mediolateral planes through the proximal and distal ends of the humerus are approximately parallel to one another in *Marasuchus*, *Herrerasaurus*, and basal ornithischians. In other words, when viewed proximally or distally, the ends of the humerus lie in about the same plane. The condition in at least some sauropodmorphs (TMM 43646-58), *Eoraptor*, and most basal theropods (including coelophysoids) is derived in that the axes of the proximal and distal ends of the humerus are distinctly offset from one another (Fig. 64). The humerus therefore exhibits torsion about its long axis relative to the ancestral condition. The derived torsion of the humerus is not present in *Ceratosaurus*, *Carnotaurus*, and *Masiakasaurus* (Bonparte et al., 1990; Madsen and Welles, 2000; Carrano et al., 2002). Humeral shaft torsion was coded as absent in all coelophysoids, *Ceratosaurus*, *Elaphrosaurus*, abelisaurids, and only present in some of the tetanuran taxa in the analysis of Carrano et al. (2002).

173. Humeral distal condyles rounded (0), or flattened (1) (Carrano et al., 2002).

174. Deltopectoral crest extends distally 30%<45% humeral length (0), or ≥45% humeral length (1), or is small, only a low triangular eminence (2) (Sereno et al., 1998; Rauhut, 2003). (UO)

This character was erected by Sereno et al., (1998) to test the existence of a clade of basal tetanurans including *Torvosaurus*, spinosaurids, and others. The character was included in the analysis of Carrano et al. (2002), who scored it against more basal theropods, including coelophysoids, *Ceratosaurus*, *Elaphrosaurus*, and abelisaurids, as well as some basal tetanurans (but not spinosaurids). The character was coded as present in *Elaphrosaurus*, *Carnotaurus*, and *Majungatholus* among the non-tetanuran theropods in that study. However, the description and illustration of the humerus of *Elaphrosaurus* does not support the presence of such a long deltopectoral crest, and I score this character absent in the taxon. The deltopectoral crest is also less than 45% overall humerus length in *Aucasaurus* (Fig. 65B) (Coria et al., 2002).

175. Radius length ≥50% (0), or < 50% (1) humerus length (Sereno et al., 1998; Holtz, 1998).

176. Radius and ulna distal articular surfaces not enlarged (0), or large and subhemispherical (1).

The disarticulated forelimb of *Carnotaurus* provided all the information about this highly derived part of abelisaurid anatomy until the recent discovery and description of the articulated forelimb of *Aucasaurus garridoi* (Coria et al., 2002). In both taxa the

distal ends of the ulna and radius bear exceptionally large, subhemispherical articular surfaces (Fig. 65A-C). The distal articular surfaces of the ulna and radius in most dinosaurs are convex, but never as well formed and relatively large as in these two abelisaurid taxa.

177. Distal carpals I and II separate (0), or fuse to each other, resulting in single element proximally capping metacarpals I and II (1) (Gauthier, 1986).

178. Distal ends of metacarpals dorsally rounded, smooth (0), or with deep, well-developed extensor pits (1) (Sereno et al., 1993).

179. Manual digit I proportions normal, with functional phalanges (0), or digit reduced to sub-conical, blocky metacarpal that lacks distal articular condyles and phalanges (1).

As mentioned above, *Carnotaurus* provided all the information about the highly derived abelisaurid forelimb anatomy until the description of the articulated forelimb of *Aucasaurus garridoi* (Coria et al., 2002). The articulated manus of the latter taxon suggests the tentative reconstruction of the manus of *Carnotaurus* (Bonaparte et al., 1990) needs minor revision. The elements previously identified as carpals (Bonaparte et al., 1990) are more likely phalanges (Coria et al., 2002). The largest element in the manus of *Carnotaurus* (identified as the fourth metacarpal by Bonaparte et al., 1990), is blocky, tapers distally, and lacks phalanges, whereas the first metacarpal is the largest

element in the manus of *Aucasaurus* (Fig. 65A-C). It is also blocky, tapers distally, and lacks phalanges. It is likely that the disarticulated element tentatively identified by Bonaparte et al., (1990) as the fourth metacarpal is actually the first metacarpal, reflecting the condition present in *Aucasaurus*. This derived condition is currently shared in only these two taxa in the present study, although future abelisaurid finds will hopefully provide additional opportunity to test the legitimacy of this character.

180. Metacarpal I and II contact at proximal bases only (0), or proximal half or more of metacarpal I closely appressed to metacarpal II (1) (Gauthier, 1986).

181. Metacarpal I with symmetrical distal articular condyles (0), or strongly asymmetrical distal articular condyles, medial condyle more proximal than lateral condyle (1) (Rauhut, 2003).

182. Phalanx I-1 length/metacarpal I length ≤1.0 (0), or >1.0 (1) (Rauhut, 2003).

183. Manual digit III (0), or manual digit II (1) is longest of the manus (Gauthier, 1986).

184. Manual digit II penultimate phalanx (II-2) length ≤ (0), or > (1) length of phalanx II-1 (Rauhut, 2003).

185. Manual digit III penultimate phalanx (III-3) length ≤ (0), or > (1) length of each of the more proximal digit III phalanges (Rauhut, 2003).

186. Metacarpal IV subequal to metacarpal III (0), or much smaller than metacarpal III (1) or absent (2) (Gauthier, 1986). (O)

Previous workers tended to lump a number of potentially independent characters pertaining to the reduction and eventual loss of the fourth manual digit through the evolution of Theropoda (Gauthier, 1986; Holtz, 1998; Sereno, 1999a; Carrano et al., 2002; Rauhut, 2003). The characters are split up here to evaluate them individually. There is subjectivity in evaluating the degree of reduction of metacarpal IV relative to the other metacarpals. For example, the cross-sectional girth of the fourth metacarpal is nearly as great as the minimum cross-section of the third metacarpal in *Dilophosaurus* (UCMP 37302). The fourth metacarpal measures roughly two-thirds or greater the length of metacarpal III in *Dilophosaurus* (UCMP 37302), *Coelophysis* (AMNH 7224), and *Syntarsus rhodesiensis* (QG 1). However, the proximal and distal ends of metacarpal IV are only weakly enlarged if at all in these taxa. The lesser girth and length relative to metacarpal III qualifies the fourth metacarpal being described as 'reduced'.

In most coelophysoids the fourth metacarpal has only a rudimentary distal articular surface for the first phalanx. The holotype of *"Syntarsus" kayentakatae* preserves part of a manus (Fig. 66A), including digit IV. Metacarpal IV is relatively shorter and more robust than in other coelophysoid taxa, being only slightly longer than half the length of metacarpal III. Also, the distal end of metacarpal IV bears a bicondylar

ginglymus that articulates with a well-formed double cotyle on the proximal end of phalanx IV-1 (Fig. 66B). There is a very faint depression for collateral ligaments visible on the exposed medial or lateral side of the distal end of metacarpal IV. Both of the latter features are unknown on this metacarpal in other theropods.

There is a vestigial second phalanx (IV-2) distal to the first (IV-1) in MNA V2623 (Fig. 66B). The element was noted first by Rowe (1989), who stated the piece in question was either a second phalanx or broken piece of phalanx IV-1. Tykoski (1998) concluded the off-angled piece represented the broken and displaced distal tip of phalanx IV-1. Further examination of the specimen revealed a small articular surface separating the elements in question, showing the conclusion of Tykoski (1998) was incorrect. No other theropod retains even a remnant of phalanx IV-2. Its presence in this specimen of *"Syntarsus" kayentakatae* could be the result of individual variation, or it could be a feature unique to the taxon. The taxon is coded as having more than one phalanx on digit IV (see below).

187. Manual digit IV with >1 (0), or ≤1 (1) phalanx (modified from Gauthier, 1986; Rauhut, 2003).

188. Manual digit V with prominent metacarpal and ≥1 phalanx (0), or is at most a vestigial metacarpal that lacks phalanges (1), or is absent (2) (Gauthier, 1986). (O)

189. Pelvic bones remain separate (0), or co-ossify with one another (1) by adulthood (Rowe, 1989; Rowe and Gauthier, 1990).

The extensive fusion between the pelvic bones present in ceratosaur taxa was recognized as a unique, identifying feature since the pelves of *Ceratosaurus* were discovered (Marsh, 1884; Gilmore, 1920). The ontogenetic analysis (Chapter 1) shows that the degrees of co-ossification and closure of sutures in the pelvis depend upon the ontogenetic status of the individual specimen. At the very least, co-ossification begins at some point in sub-adulthood, as indicated by specimens of *"Syntarsus" kayentakatae* (TMM 43688-1) and the Shake-N-Bake taxon. Closure of pelvic sutures may not be complete (=fusion) until late in ontogeny, as shown by other Shake-N-Bake specimens.

This character was deleted from the phylogenetic analysis of Rauhut (2003) because it was ontogenetically variable. Among more basal theropods and basal tetanurans only a few taxa known from adult individuals exhibit such a high degree of pelvic co-ossification. Analysis of coelophysoid theropods (Chapter 1, Table 3) shows pelvic co-ossification occurred relatively early in ontogeny within the coelophysoid clade. This contrasts with the pattern seen in many tetanurans. In those few large tetanurans known from multiple specimens across an ontogenetic series (e.g., *Allosaurus*, some tyrannosaurids), pelvic co-ossification is either not present or it is weakly expressed only in some large adults (Osborn, 1917; Madsen, 1976; Maleev, 1974; Brochu, 2002). The different ontogenetic pathways taken in the pelvic girdles of coelophysoid and tetanuran theropods represents a phylogenetically informative character and should be incorporated into analyses of basal theropod relationships.

It was claimed (Rauhut, 2003) that the pelves of the types of *Ceratosaurus nasicornis* and *Elaphrosaurus bambergi* are only partially fused, and different modes of fusion are present in each. There appears to be little pelvic fusion present in the type of *Elaphrosaurus* as evidenced by the original description and figures of the specimen (Janensch, 1925:figs. 8, 14; pl. 3) and in photographs generously provided by P. Makovicky (pers. comm., 1997). Both ischia were co-ossified, but by description only the right ischium even remained in contact with its respective ilium after death. The incomplete left pubis of the specimen shows no sign of co-ossification with either the ilium or the left ischium. The presence of fused cervical ribs, vertebral neural arches and centra, sacral vertebrae, and the sacrum to the ilia seems incongruent with the lack of pelvic co-ossification. Until the entire specimen is evaluated in an ontogenetic analysis it is difficult to assess whether this represents a strictly ontogenetic aspect of the individual, or if the lack of pelvic co-ossification in the specimen is of phylogenetic importance. The character is coded as missing data for this taxon.

The pelvis of the type of *Ceratosaurus* (USNM 4735) is far more extensively fused than that of *Elaphrosaurus*. The degree of pelvic co-ossification in this specimen is among the most extensive of any non-maniraptoran theropod, with the exception of some coelophysids (Gilmore, 1920). The contacts between the ilia and the pubes, as well as between the ilia and ischia are fused so sutures are difficult to identify. The contact between the pubis and ischium is visible as a noticeable suture in the puboischiadic plate. It is assumed that the presence of a visible suture between the pubis and ischium prompted the claim that the pelvis was only partially fused in this specimen.

The lack of pelvic co-ossification in *Liliensternus*, *Gojirasaurus*, and *Dilophosaurus* was also used by Rauhut (2003) to invalidate the importance of this character in theropod phylogeny reconstruction. The implication was that the character was only sparsely distributed even among purported ceratosaur taxa, and as such was of little or no utility. Again, this approach ignored the ontogenetic stages represented by the respective specimens of these taxa. The material referable to *Liliensternus* possesses numerous signs of relative immaturity. *Gojirasaurus* is known from little more than some teeth, a couple of dorsal vertebrae (with detached neural arches), a partial scapula, a pubis, and a tibia. Given the hypothesized pattern of ontogenetic development for coelophysoids (Table 3) it is likely that this individual was still immature.

Claims that the pelvic bones of *Dilophosaurus* did not fuse are based upon the immature type and referred specimens (UCMP 37302, 37303). Another referred specimen (UCMP 77270) was an adult individual and preserves an incomplete synsacrum. The partial left ilium and the proximal end of the left pubis are present and firmly fused to one another. Although the area of contact between the two bones is badly weathered, only a faint suture is discernable between the two elements. It is clear that at least these pelvic bones did fuse by adulthood, and the character is coded as present for the taxon.

190. Ilium anteroposterior length shorter (0) or about as long or longer (1) than femur: (Holtz ,1998).

191. Dorsal margin of ilium dorsally convex and obviously curved (0), or relatively linear/angular (1) (modified from Carrano et al., 2002).

The dorsal margin of the ilium defines a gently curved, dorsally convex profile in the basal members of the major dinosaur clades. The degree of dorsal arcing varies from only weakly convex in basal ornithischians, sauropodomorphs, and basal tetanurans, to strongly convex in *Ceratosaurus* (Fig. 67A, B). In contrast, the ilium dorsal margin is relatively straight-edged in *Coelophysis*, *Syntarsus rhodesiensis*, *"Syntarsus" kayentakatae*, *Elaphrosaurus*, *Carnotaurus*, *Majungatholus*, and *Aucasaurus* (Figs. 67C, D). This does not mean that the ilium is absolutely straight from anterodorsal to posterodorsal corners. Instead, the ilium remains low and may have relatively angular changes in its dorsal profile. The ilium of the type of *Syntarsus rhodesiensis* (QG 1) was illustrated with a nearly straight dorsal border (Raath, 1969, 1977). Other specimens (QG 691; Raath, 1977:pl. 19c) have a morphology more similar to that of *Coelophysis* and *Dilophosaurus*.

The ilium of *Dilophosaurus* was illustrated with a high, arcing profile by Welles (1984). What was not made clear at the time was that the anterior half of the ilium was reconstructed, and that the complete morphology of the ilium was not known (Fig. 67E). This led to subsequent workers' assumption that the ilium in *Dilophosaurus* was as strongly arched as in *Allosaurus* and basal tetanurans. The ilia of the TMM *Dilophosaurus* (TMM 43646-59, TMM 43646-60) are very low and straight-edged, with a posteroventral dip in the dorsal profile above the ischial peduncle (Fig. 67F). They strongly resemble the ilium in *Coelophysis*, *Syntarsus rhodesiensis*, and *"Syntarsus"*

kayentakatae. The middle third of the partial ilium of UCMP 77270 also has a linear dorsal margin. I code this character present in *Dilophosaurus*.

The ilium of *Liliensternus* was illustrated with a gentle dorsally convex margin (Huene, 1934). However, there are substantial parts of both right and left ilia missing from the specimens figured by Huene (1934), and the intervening sections have proportions very similar to those of *Dilophosaurus*. This character is scored present for *Liliensternus*. The dorsal edge of the ilium in *Elaphrosaurus* was coded as strongly convex by Carrano et al. (2002), even though the profile of the ilium is only slightly more arced than that of *Majungatholus*, which they scored as linear. Both taxa are coded having a linear dorsal margin of the ilium.

192. Preacetabular process of ilium does not extend past pubic peduncle (0), or extends anteriorly well past pubic peduncle (1) (Gauthier, 1986; Carrano, 2000).

193. Preacetabular process of ilium stout and thick (0), or relatively thin and blade-like (1).

The preacetabular process of the ilium is a relatively short protuberance or spine in *Marasuchus*, *Herrerasaurus* and basal sauropodomorphs (Fig. 68A). It is longer in *Lesothosaurus* and *Scutellosaurus*, but remains very narrow and rod-like in these basal ornithischians. In the type of *Eoraptor* the preacetabular process remains short, but it is mediolaterally flattened, blade-like, and more dorsoventrally expanded than in the aforementioned taxa (Fig. 68B, C). The process remains blade-like in all more derived

theropods, with much greater dorsoventral expansion of the blade in these taxa (Fig. 68D).

194. Ventral rim of preacetabular process of ilium relatively horizontal (0), or with ventral expansion or 'hook' (1) (modified from Gauthier, 1986; Sereno et al. 1994).

195. Supraacetabular crest of ilium a weakly developed ridge or raised shelf (0), or flares lateroventrally to form hood-like overhang that hides anterodorsal half of acetabulum in lateral view (1).

The supraacetabular crest is a large shelf that projects laterally from along the anterodorsal margin of the acetabular recess. The crest formed a strong buttress against which the proximal end of the femur and the associated joint capsule was braced. Many descriptions have been used in cladistic character sets to categorize the form of this structure. The potential character states for this structure were listed as "pendant" and "shelf-like", with the former as the ancestral condition for Theropoda and present in *Eoraptor*, *Herrerasaurus*, coelophysoids, *Ceratosaurus*, *Elaphrosaurus*, and abelisaurids by Carrano et al. 2002. There is considerable difference between the degree of supraacetabular crest development between these taxa, especially with regard to the condition present in coelophysoid theropods. My evaluation of this character differs substantially from the scoring of previous authors.

In *Marasuchus*, *Herrerasaurus*, basal sauropodomorphs, *Eoraptor*, and many basal tetanuran taxa the crest is shelf-like, and extends mostly laterally over the

acetabulum (Fig. 69A). This leaves the acetabulum widely exposed in lateral view. The supraacetabular crest of coelophysoids is more extensively developed. It not only flares laterally but also ventrally, hiding most of the dorsal and anterior parts of the acetabulum in lateral view (Figs. 69B-D). In some specimens the crest hangs ventrally nearly to the level of the ilio-pubic contact (Figs. 69B, D).

The supraacetabular crest is large, but not hood-like in *Ceratosaurus* and the abelisaurs *Carnotaurus* and *Majungatholus*. This character is coded as absent in these taxa. In *Elaphrosaurus*, the supraacetabular crest of the left ilium may be truncated by distortion and fracturing (Janensch, 1925; fig 8). However, other figures (Janensch, 1925:pl. 3) show the crest on the right ilium continues anteroventrally down the pubic peduncle and cups over the acetabulum. In this regard *Elaphrosaurus* resembles coelophysoids and this character is coded as present in the taxon.

196. Brevis fossa of ilium narrow (0), or broad (1) posteriorly (Sereno et al. 1994, 1996).

197. Ilium postacetabular length ≤ (0), or > (1) acetabulum width (1) (Forster, 1999; Carrano, 2000; Carrano et al., 2002).

The postacetabular part of the ilium is anteroposteriorly shorter than the acetabulum in *Marasuchus*, *Lesothosaurus* (but apparently not *Scutellosaurus*), basal sauropodomorphs, and *Herrerasaurus* (Fig. 68A). The postacetabular process was scored as shorter than the acetabulum in *Eoraptor* (Carrano et al., 2002). The process is substantially longer than the acetabulum in all other theropods. Close examination of a

cast of the holotype of *Eoraptor* (TMM 43451-2, cast of PVSJ 512) reveals that the more widely exposed left ilium is badly eroded and is missing much of the postacetabular process. This gives the impression of a very short posterior process on the ilium. The right ilium is better preserved, but much of it is hidden by matrix and elements of the right hindlimb. The posterior tip of the right ilium is just visible in the cast, protruding from matrix between the tibia and fibula and the second metatarsal (Fig. 68C). Measurements taken from the acetabular width of the left ilium and from the postacetabular process of the right ilium suggest the postacetabular process was slightly longer than the anteroposterior width of the acetabulum in *Eoraptor*.

198. Posterior margin of ilium posteriorly convex or squared off (0), or concave, notched, or indentated (1) in lateral view (Tykoski, 1998; Sereno, 1999a).

The posterior margin of the ilium's postacetabular process is bluntly rounded or squared off in the majority of fossil theropods (Fig. 70A). A derived state is expressed in the ilium of abelisaurids and some coelophysoids. The posterior margin of the ilium has a posteriorly concave profile in lateral view in *Coelophysis* (AMNH 7223), *Syntarsus rhodesiensis* (QG 1 and others), *"Syntarsus" kayentakatae* (TMM 43688-1), *Elaphrosaurus*, *Carnotaurus* (MACN-CH 894), and *Majungatholus* (UA 8678) (Fig. 70B-F). This character was coded as absent in all the coelophysoids listed here by Carrano et al. (2002).

The posterior concavity of the iliac blade margin in *Majungatholus* is little more than a deep notch in the border of the bone. Similar notches were described in the ilium

of *Aucasaurus* and attributed to *Carnotaurus* as well (Coria et al., 2002). A hypothesized purpose for these distinct notches in abelisaurid ilia was to accommodate the hypertrophied, awl-like anterior processes on the distal tips of the transverse processes of the first caudal vertebra (Coria et al., 2002). No such processes are present on the anterior caudals of coelophysoid theropods.

199. Ilium with M. iliofemoralis fossa that reaches posterior rim of bone (0), or stops short of bone's posterior margin, resulting in distinct rim on lateral surface of postacetabular process (1) (modified from Rowe, 1989).

The lateral surface of the saurischian iliac blade is broadly concave dorsal to the acetabulum and supraacetabular crest. It was recognized long ago that this broad lateral fossa was occupied with a suite of dorsal thigh muscles that bore homologues to the hindlimb and pelvic anatomy of extant crocodylians and avians (Romer, 1923a, 1923b, 1923c; Rowe, 1986; Hutchinson, 2001a). Recent studies suggested that the lateral fossa on the postacetabular process of the ilium in theropods accommodated the M. iliofemoralis (Hutchinson, 2001a). The lateral fossa on the posterior part of the ilium extends to the margins of the bone both dorsally and posteriorly in most of the basal theropods (Fig. 70A, E, F).

Coelophysis (AMNH 7223, AMNH 7224, UCMP 129618), *Syntarsus rhodesiensis* (QG1), *"Syntarsus" kayentakatae* (TMM 43688-1), and the Shake-N-Bake taxon (TMM 43689-5) have a derived condition in the morphology of the postacetabular process that distinguishes them from other theropods. The lateral iliac fossa on the does

not reach the posterior margin of the ilium. Instead, the fossa stops well short of the posterior terminus of the process. The posterior margin of the fossa is clearly marked by a raised surface that extends to the posterior extremity of the iliac blade (Fig. 70B-D). Whereas the lateral surface of the ilium is smooth within the lateral fossa, the raised area at the posterior tip of the ilium in these taxa is very rough, as if it was the site of extensive connective tissue attachment (Fig. 70D). Descriptions that the ilium of *Coelophysis* lacked the distinct rim delineating the lateral iliac fossa (Colbert, 1989) are contradicted by the available material.

200. Pubic peduncle of ilium size approximately equal to (0), or much greater than (1) ischial peduncle (Sereno et al., 1994).

201. Anteroposterior length of pubic peduncle of ilium <2 times (0), or ≥2 times (1) mediolateral width (Gauthier, 1986; Carrano, 2000; Carrano et al., 2002).

202. Pubic peduncle of ilium projects ventrally about as far as (0), or much further than (1) ischial peduncle (Gauthier, 1986; Holtz, 1998).

203. Pubic peduncle of ilium with single distal facet (0), or two facets separated by kink, resulting in anterior and ventral-oriented pubic contacts (1) (modified from Sereno et al., 1998).

This character is not well understood because it is easily observed only in relatively immature coelophysoid specimens lacking co-ossification between the pelvic bones. The pubic peduncle of the ilium bears a single large ventrally directed facet for contact with the pubis in most basal theropods (Fig. 71A). There are two distinct, socket-like facets on the distal end of the ilium's pubic peduncle in coelophysoid theropods (Fig. 71B, C). The larger of the two facets faces mostly anterior and is more than twice the size of the second facet. The smaller, more posterior facet is directed ventrally. The two sockets are separated by a strong ridge that mediolaterally traverses the distal surface of the ilium's pubic peduncle (Fig. 71B). It is possible to trace the contact between the ilium and pubis in co-ossified pelves that retain open sutures, such as on the sub-adult *"Syntarsus" kayentakatae* specimen TMM 43688-1. The external expression of the open suture approximately follows the contour of the contact surfaces.

204. Ilium-pubis articulation abutting (0), or with deep peg-in-socket (socket in pubis) connection (1) (Sampson et al., 2001).

205. Proximal pubic plate ventromedial to obturator foramen solid (0), or with pubic fenestra (1), or pubic fenestra and obturator foramen intersect to form obturator notch (2) (Rowe, 1989; Rowe and Gauthier, 1990). (O)

The pubic plate (the pubic contribution to floor of the pelvic canal) of archosaurs was imperforate with the exception of the obturator foramen, and this condition was retained in basal Dinosauria (Fig. 72A-D). Some sauropodomorphs (TMM 43646-50,

43646-51), and coelophysoids have a derived condition in which an accessory foramen or fenestra opened ventromedial to the obturator foramen. This additional opening, named the pubic fenestra (sensu Camp, 1936) was considered a diagnostic synapomorphy of Ceratosauria by Rowe (1989), and Rowe and Gauthier (1990). Other authors questioned the validity of the character, as well its distribution among the taxa cited by Rowe (1989) and Rowe and Gauthier (1990). The character was adopted by Holtz (1998), but excluded from the analyses of Carrano et al. (2002) and Rauhut (2003).

The most recent comprehensive review of the evolution of pelvic osteology and its soft-tissue correlates along the archosaurian lineage leading to Aves was conducted by Hutchinson (2001a). Among the anatomical features addressed in the work was the opening of the obturator notch. It was pointed out that the obturator notch represented the loss of the ossified ventral and medial borders of the obturator foramen. This had the effect of connecting the pubo-ischiadic fenestra, obturator foramen, and pelvic fenestra in relatively derived tetanuran taxa. The presence of an accessory foramen in the pubic plate of coelophysoid theropods was noted by Hutchinson (2001a), but only as a brief reference to the appearance of the opening and its relationship to pelvic anatomy in more derived taxa. I hypothesize that the pubic fenestra of Rowe (1989) and Rowe and Gauthier (1990) represents part of a morphological continuum of puboischiadic plate reduction that occurred on the lineage leading to Aves.

The puboischiadic plate is extensive and ossified in *Marasuchus* (Fig. 72A, B), *Herrerasaurus* (Fig. 72C, D), and basal sauropodomorphs. In at least *Marasuchus* and *Herrerasaurus* the pubic plate extends anteriorly all the way from the pubis-ischium

contact to the proximal pubic shafts. The osseous lamina then continues distally as the more transversely oriented pubic apron (Fig. 72B, D). A similar condition is also present in the basal tetanuran *Torvosaurus* (Fig. 72E).

A very different morphology is present in many other tetanuran theropods, such as *Allosaurus* (Fig. 73A-C). The floor of the pelvic canal is unossified, open ventrally, and extends from the relatively distal obturator process on the shaft of the ischium to the proximal edge of the pubic apron between the pubic shafts. The pubis and ischium only contact just ventral to the acetabulum. Their suture does not extend ventromedially toward the midline.

Ceratosaurus, *Segisaurus*, *Dilophosaurus*, *Syntarsus rhodesiensis*, *Coelophysis*, and the Shake-N-Bake taxon exhibit important intermediate stages of the reduction of the osseous pelvic canal in Theropoda. The left and right pubic plates meet proximally along the midline ventromedial to the obturator foramen in these taxa, much like in *Marasuchus* and *Herrerasaurus* (Figs. 72, 74A, B). Unlike the condition in *Marasuchus*, *Herrerasaurus*, and *Torvosaurus*, the pubic plate is not continuous from the pubis-ischium contact to the distal part of the pubic shaft. Instead, the medial edge of each pubis arcs away from the midline for a short interval just distal to the obturator foramen. The margin of the pubic plate then curves back distomedially to meet its counterpart again between the pubic shafts. This rim forms the proximal edge of the pubic apron. The opening in the pubic plate that results from the lateral-ward embayment of the pubes' medial margins is the pubic fenestra (Camp, 1936; Rowe, 1989; Rowe and Gauthier, 1990) (Fig. 74A, B).

The perforation of the pubic plate is different in *Syntarsus rhodesiensis*. Two enclosed foramina were reported in the proximal pubis of *Syntarsus rhodesiensis* (Raath, 1969, 1977). Illustrations and photographs of the type specimen (QG 1) show the ventral margin of the pubic plate is incomplete, including the posteroventral edge of the pubic fenestra (Fig. 74C). However, at least one other specimen (QG 691) preserves a fully enclosed pubic fenestra in the pubic plate. A similar morphology was illustrated by Rowe and Gauhtier (1990) for *Coelophysis*, but no specimen number was cited for the basis of the illustration (Fig. 74D). There is no bony ventromedial border of the pubic fenestra in *Ceratosaurus* (Fig. 74A, B), *Segisaurus* (Fig. 75A, B).

The proximal pubes of *Dilophosaurus* were described and figured by Welles (1984) from the type specimen of the taxon (UCMP 37302). The description at that time stated that there was no obturator foramen in the pubis of *Dilophosaurus*. However, recent examination of the type specimen turned up no sign of the proximal pubes. Conversation with the individual who supervised the original mounting of the skeleton indicated the proximal pubes were not present at that time, and evidently were not preserved or collected with the specimen (W. Langston, pers. comm., June 2003). Instead, the proximal part of each pubis was restored in plaster, and was modeled after pubes of other theropods such as *Allosaurus*. Analyses that coded the obturator foramen in *Dilophosaurus* as absent or open were likely based upon this reconstruction.

A nearly complete pubis of *Dilophosaurus* is now known from the Texas Memorial Museum *Dilophosaurus* Quarry in the Gold Spring Area of the Kayenta Formation. The specimen (TMM 43646-79) preserves the medial margin of the pubic

contribution to the puboischiadic plate (Fig. 75C). A completely encircled obturator foramen is present, as well as the rim of the pubic fenestra.

Pubes of *Coelophysis* (MCZ 4330) and the Shake-N-Bake taxon (MCZ 9443) preserve the dorsal borders of a pubic fenestra (Fig. 75D). The ventromedial parts of the pubic plates in the latter specimens are inadequately preserved to determine whether or not their pubic fenestrae were fully enclosed as in *Syntarsus rhodesiensis*, or open along the midline as in *Segisaurus*, *Ceratosaurus*, and *Dilophosaurus*. The proximal rim of a pubic fenestra is also preserved in the pubis of *Gojirasaurus* (Carpenter, 1997). The proximal pubes of *Liliensternus* were figured by Huene (1934:pl. 15, figs. 9a, 9b) and show the dorsal rim of a small, ovoid obturator foramen. The more medioventral part of the proximal pubis appears to be missing. Given the well-defined partial rim of a foramen here, it is likely there was an enclosed obturator foramen in *Liliensternus*, much like in *Dilophosaurus*, *Gojirasaurus* (Carpenter, 1997), and all other coelophysoids that adequately preserve this area. However, it is uncertain if *Liliensternus* had a pubic fenestra, based on the available specimens.

The pubic fenestra represents the initial stages of reduction of the proximal pubic plate in Theropoda. A hypothesis of the sequence of pubic fenestra formation is as follows. First, thinning of the pubic plate anteroventral and medial to the obturator foramen resulted in opening of an accessory foramen, an enclosed pubic fenestra, such as that in *Syntarsus rhodesiensis*. Continued enlargement of the fenestra in each pubis eventually brought each into intersection with the medial edge of their respective pubes. The two openings combined to form a single separation between the part of the pubic

plate along the ischial contact and the part that continued distally as the pubic apron. The pubic fenestra remained separated from the pelvic fenestra (sensu Hutchinson, 2001a) in these taxa by the median contact of the pubes between the two fenestrae.

It took relatively few steps to go from the morphology of the proximal pubis present in the coelophysoids and *Ceratosaurus* to that found in *Allosaurus* and other tetanurans. The obturator foramen is the osteological passageway for the N. obturatorius, and is located in the proximal pubis anterorventral to the acetabulum (Hutchinson, 2001a). It is fully encircled by bone in Archosauria ancestrally, a condition retained in basal Dinosauria (Romer, 1956). An enclosed obturator foramen is present in basal theropods, including *Eoraptor* (Fig. 75E), coelophysoids (Figs. 74C, D, 75A-D), *Ceratosaurus* (Fig. 74A, B), abelisaurs (Fig. 70E), and some basal tetanurans (Fig. 72E). As described above, the pubic fenestra appeared ventral and medial to the obturator foramen as part of the great reduction of the puboischiadic plate through theropod evolution. The pubic fenestra eventually enlarged until it breached the ventral border of the obturator foramen. The resulting embayment in the ventral margin of the proximal pubis is commonly referred to as the obturator notch. This character state is present in at least *Allosaurus* in this analysis (Fig. 73).

The pubic fenestra and pelvic fenestra eventually intersected, opening the floor of the pelvic canal from the proximal edge of the pubic apron to the obturator processes of the ischia. The pubic fenestra was not technically lost in tetanuran taxa such as *Allosaurus* or *Ornitholestes*. It merely enlarged until the osseous borders were breached between it, the obturator foramen, and pelvic fenestra. Just as the obturator notch of

many tetanurans is the homologue to an enclosed obturator foramen, the homologue of the pubic fenestra (sensu Camp, 1936; Rowe, 1989; Rowe and Gauthier, 1990) is present in most tetanuran taxa. It is the open space just proximal to the pubic apron, which is continuous with the pelvic fenestra and obturator notch (Fig. 73). A ventrally open pubic fenestra is present in *Allosaurus* and *Ornitholestes*, but there is not a pubic fenestra in *Torvosaurus* among the tetanurans in my analysis.

A pubic fenestra is also present in *Eoraptor*, based upon examination of TMM 43451-2 (cast of holotype skeleton PVSJ 512). Parts of the pubic plate were covered with clay or other putty-like material prior to the molding and casting of the specimen. The holotype's right pubis is well preserved and exposed (Fig. 75E). Two natural foramina perforate the pubic plate. The more dorsal and lateral foramen was filled with clay prior to molding, but it corresponds in position, form, and relative size to the obturator foramen of other theropods. The rim of the second opening is clearly visible ventral and medial to the obturator foramen. The latter corresponds in position and appearance with the pubic fenestra of other theropods, and is identified as such here. The anterior half of the pubic fenestra was covered with clay prior to casting, but the ventral and medial edges of the opening are visible. The pubic fenestra does not reach the median edge of the pubic plate such as in *Syntarsus rhodesiensis*, but unlike the condition in *Segisaurus*, *Dilophosaurus*, and *Ceratosaurus*, (Raath, 1969, 1977).

206. Mediolateral width of pubic midshaft ≥25% (0), or <25% (1) overall shaft length.

The pubic shafts of *Marasuchus*, *Plateosaurus*, *Herrerasaurus*, and *Eoraptor* are all transversely broad, with large pubic aprons. The mediolateral width of the pubic shaft is more than 25% the overall length of the pubic shaft in these taxa (Fig. 72B, D). More derived theropods have much narrower pubes, less than 25% the proximo-distal length of the pubic shaft (Figs. 73C, 74B, 77C). The character is also present as the thin, rod-like, and posteriorly directed pubes in *Lesothosaurus* and *Scutellosaurus*, but its presence in these taxa is viewed here as an independent acquisition.

207. Axis of pubic shaft straight or curves anteriorly (0), or curves ventrally, resulting in anterior bowing (convex anterior, concave posterior) of shaft in lateral view (1) (Rowe, 1989).

The long axis of the pubic shaft is ventrally curved in the ornithodiran *Marasuchus* (Fig. 72A), but it is almost straight in *Lesothosaurus*, *Scutellosaurus*, *Plateosaurus* and other basal sauropodomorphs, abelisaurids (Fig. 70E), and most basal tetanurans (Fig. 73A, B). The pubis of *Herrerasaurus* projects ventrally, but the long axis of the shaft itself is straight (Fig. 72C). The shaft of the pubis of *Eoraptor* is ventrally curved based upon a cast of the holotype (TMM 43451-2), as is the pubis of *Ceratosaurus* (USNM 4735), *Masiakasaurus* (FMNH PR 2108), *Dilophosaurus* (TMM 43646-79), *Coelophysis* (AMNH 2706, 7223, 7224, MCZ 4330, others), *"Syntarsus" kayentakatae* (MNA V2623, TMM 43688-1), *Syntarsus rhodesiensis* (QG 1, QG 691, others), *Gojirasaurus* (UCM 47721), *Procompsognathus*, and the Shake-N-Bake taxon.

The degree to which the pubic shaft bows varies between these taxa. The shaft is strongly bowed anteriorly in lateral view in *Ceratosaurus* (Fig. 72A) *Coelophysis* (Fig. 74D), *Syntarsus rhodesiensis* (Fig. 74C), and *"Syntarsus" kayentakatae* (Fig. 76A). The pubis of *Ceratosaurus* was coded as straight by Carrano et al. (2002), but illustrations show the pubic shafts of the holotype are strongly downcurved. The pubic shaft is only weakly curved in *Masiakasaurus* (Fig. 76B), *Dilophosaurus* (Fig. 76C), *Liliensternus* (Fig. 76D), and *Gojirasaurus*. This probably led to interpretation of a straight pubic shaft in these taxa (Carrano et al., 2002).

The pubic shafts of *Segisaurus* are preserved in the only known specimen, but they are broken in mid-length and dorsoventrally compressed. It is difficult to determine if the pubic shaft axis is bowed in the anterior direction or not. The character is coded as missing data for *Segisaurus*. The pubis of *Elaphrosaurus* was scored as straight in recent analyses (Carrano et al., 2002; Rauhut, 2003). The distal half or more of the pubic shaft is missing for *Elaphrosaurus*, and the character is coded as missing data here.

208. Medial lamina of pubis that reaches distal tip of shaft (0), or stops short of distal tip of pubic shaft, resulting in short median separation between distal tips of pubes (1).

The pubic apron is formed by thin laminae that extend medially from the main pubic shaft, and meet along a median contact. The apron extends the length of the pubic shaft in *Marasuchus*, *Herrerasaurus*, *Plateosaurus* and other basal sauropodomorphs, and *Eoraptor* (Figs. 72B, 77A). Most other theropods for which adequate material is known have some degree of median separation between the distal ends of the pubes. The

pubic apron stops short of the distal tips of the pubis, while the robust lateral part of the pubic shaft continues distally. The distal median separation is most recognizable in those taxa that lack an enlargement on the distal tip of the pubic shaft, or pubic boot. The pubic apron extends far distally in the coelophysoids *Segisaurus*, *Liliensternus*, *Coelophysis*, and *"Syntarsus" kayentakatae*, so that the distal tips of the pubic shafts are separated by only a short, rectangular notch in anterior view (Fig. 77B, C). The pubic apron stops more proximally in *Dilophosaurus*, resulting in an elongate distal notch or gap between the distal pubis tips (Fig. 77D). The pubes of *Syntarsus rhodesiensis* were illustrated with the pubic apron extending to the distal terminus of the pubes (Raath, 1977). If this is accurate it is an unusual condition given the distribution of this character among other coelophysoids.

The pubic apron stops at a more proximal point in many tetanuran taxa. In addition, the distal tips of the pubes are often greatly expanded in tetanurans, to the point that the right and left pubes may re-establish a median contact at their distal tips. The resulting foramen or gap between the pubic apron and the distal pubic expansion was labeled the pubic foramen (Hutchinson, 2001a) (Figs. 72E, 73C). The pubic foramen is large in *Allosaurus*, but is very small in *Torvosaurus* (Galton and Jenson, 1979:fig. 2E, F). The pubis of *Baryonyx* is not well preserved, but given the distal morphology of the pubic shaft it is unlikely that the tips contacted to encircle a pubic foramen.

The pubes of the type specimen of *"Syntarsus" kayentakatae* (MNA V2623) have small expansions at the distal tips that are in contact (Fig. 77C). The pubes of the specimen underwent a small amount of mediolateral compression and overlap, and the

left pubis shaft was rotated almost 45 degrees counterclockwise relative to the right pubic shaft. As as result, the distal expansions are turned toward each other and come into contact posteriorly in an unnatural manner. I do not consider the opening between the pubic apron and the terminal expansions of this specimen a true pubic foramen. Contact between the distal pubic expansions is also present in at least one specimen referred to *Coelophysis* (UCMP 129618) (Padian, 1986). I hesitate to accept this feature as a true pubic foramen until the possibility of distortion similar to that in the *"Syntarsus" kayentakatae* specimen MNA V2623 is ruled out.

Recent cladistic analyses noted the presence or absence of contact between the distal tips of the pubes, and the presence or absence of a pubic foramen (Holtz, 1998; Carrano et al., 2002; Rauhut, 2003). However, the evidence indicates the pubic foramen may be an incidental result of two independently evolving variables. The first is the proximal-ward retreat of the distal edge of the pubic apron from the distal tips of the pubes. The second is the expansion of the tips of the pubes, which in some taxa is great enough to result in re-establishment of contact between the two elements at the distal tips. Instead of scoring the presence or absence of a pubic foramen these two variables are each addressed independently in my analysis by this and the following character.

209. Distal tips of pubes with median contact (0), or without median contact (1) (modified from Holtz, 1998; Rauhut, 2000).

210. Distal tip of pubis lacking substantial anteroposterior enlargement (0), or enlarged 2<3 times (1) or ≥3 times (2) anteroposterior width of pubic shaft (modified from Rauhut, 2003). (O)

The distal expansion of the pubic shaft was long recognized as a potentially informative phylogenetic character (Gauthier, 1986; Holtz, 1998; Carrano et al., 2002; Rauhut, 2003). It has proven difficult to describe and verbalize for various reasons. One reason is that some workers simply scored the presence of a 'rounded knob' versus a 'pubic boot', without clearly explaining what size and shape of expansion constituted a 'boot' and what was merely a 'rounded knob'. Another reason is that there is substantial variation in the details of the distal pubic expansion. Some have a long median contact and combine to form a large triangular structure (e.g., *Allosaurus*), while others remain more or less separate bosses on the distal pubes (e.g., *Torvosaurus*). Some are distinct but small structures (e.g., *"Syntarsus" kayentakatae*), while others are very large (e.g., *Herrerasaurus*). The result is the potential for two workers to view the same specimen and score it differently based upon their notion of what constitutes a distal expansion of the pubis.

For the purpose of this work, the term 'pubic boot' refers to an anteroposterior expansion of the distal terminus of the pubic shaft that is two or more times as wide as the anteroposterior width of the pubis at mid-shaft. This applies to more taxa than have traditionally been scored as having a pubic boot, such as coelophysoids. Most coelophysoids have a small distal expansion of the pubic shaft which is probably homologous with the much larger pubic boots of more derived theropods. The major

difference is the size of the expansion, and there is no explicit minimum size given in the literature that qualifies a distal expansion as a pubic boot. There is also no requirement that the distal expansions of the pubes meet along the median plane to qualify as a boot.

There is no pubic boot present in *Marasuchus*, basal ornithischians, *Plateosaurus* and other basal sauropodomorphs, or *Eoraptor*. The pubis of *Herrerasaurus* has a very large pubic boot, as relatively large as that found in derived tetanurans. The pubes of *Dilophosaurus*, *Coelophysis*, *"Syntarsus" kayentakatae*, and *Liliensternus* each have a distal expansion that is between two and three times the anteroposterior width of the pubic shaft (Fig. 78A, B). This is contrary to coding of this character by Rauhut (2003), who considered this character present only in *Dilophosaurus* among the coelophysoids listed above. The distal pubis of *Segisaurus* bears small expansions (Fig. 77B), but the lateral margins of both pubes are hidden by sediment and the relative sizes of the pubic components cannot be measured. There is apparently little or no distal expansion of the pubis in *Syntarsus rhodesiensis* (Raath, 1969; 1977) or *Gojirasaurus* (Carpenter, 1997).

The distal pubic boot in *Dilophosaurus* is tentatively scored as less than three times as wide as the pubic shaft. However, the distal end of the right pubis of UCMP 37303 is nearly three times wider than the most proximal part of the preserved piece (Fig. 78A). If the size of the pubic boot is in part a factor of the ontogenetic stage of the individual, then it is very possible that the pubic boot of an adult *Dilophosaurus* could be three or more times the width of the shaft. The distal pubis is expanded to three or more times the anteroposterior thickness of the pubic shaft in *Carnotaurus*, *Aucasaurus*, *Eustreptospondylus*, and *Allosaurus*. The type specimen of *Ceratosaurus nasicornis* did

not preserve the distal end of the pubes, and these were restored based upon contemporary theropods such as *Allosaurus*. Recent discoveries indicated there is a substantial, posteriorly extended boot on the distal pubis, and that the relative size of this structure varies with ontogeny (Britt et al., 1999, 2000). The preservation of the pubis of *Baryonyx* makes it difficult to determine the actual relative proportions of the distal end versus the midshaft width. The pubis of *Suchomimus* is evidently more complete, and the size of the distal expansion appears small in the skeletal reconstruction of the known material (Sereno et al., 1998).

211. Distal expansion of pubis continuous with or expanded laterally beyond margin of shaft (0), or medially inset from lateral edge of pubic shaft (1).

The pubic boot of most theropods is either continuous with the lateral surface of the pubic shaft, or it expands laterally beyond the surface of the pubic shaft (Fig. 78). The structure of the pubic boot is derived in *Masiakasaurus*, *Carnotaurus*, and *Aucasaurus*. The posterodorsal margin of the boot is medially inset from the lateral surface of the pubic shaft and the distal surface of the pubic boot (Fig. 79A, B). The published literature gives no indication of whether the pubic boot of *Ceratosaurus* shares this apomorphic condition, and the character is scored as missing data for the taxon.

212. Distal tip of pubis elongate rectangular or subequant (0), or subtriangular (1) in distal view (modified from Rauhut, 2003).

The subtriangular profile of the distal pubis was considered a primitive state for dinosaurs by Rauhut (2003), based on the presence of this morphology in *Coelophysis* and other taxa that lacked a substantially enlarged distal pubic expansion. This reasoning was flawed given the non-triangular pubic distal termini in *Marasuchus*, basal ornithischians, *Plateosaurus* and other basal sauropodomorphs (but present in *Saturnalia* [Langer, 2003]), *Herrerasaurus*, and *Eoraptor* (Fig. 80A). The distal end of the pubis has a subtriangular to triangular profile in most coelophysoids, abelisauroids, and tetanurans (Fig. 80B). The character is therefore potentially diagnostic of all theropods more derived than *Eoraptor*. The expansion of the distal pubis is not subtriangular in the type of *"Syntarsus" kayentakatae* (Fig. 80C). Instead, the distal pubic boots are mediolaterally narrow, and angle distally toward the median plane.

213. Ischium length >2/3 (0), or ≤2/3 (1) the length of pubis (Gauthier, 1986).

214. Ischial antitrochanter small, indistinct (0), or large and protrudes anterolaterally into acetabulum, giving 'notched' profile to posteroventral margin of acetabulum (1) (Rowe and Gauthier, 1990; Sereno, 1999a).

This character requires clarification and explicit description. The presence of a large ischial antitrochanter was considered the primitive state among theropods by Carrano et al (2002). This is the opposite polarity from its use by previous workers (Rowe, 1989; Rowe and Gauthier, 1990; Holtz, 1998). The ischial part of the pelvic antitrochanter is little more than a faint area of textural difference that may be raised

slightly above the surface of the surrounding bone in basal sauropodomorphs, *Herrerasaurus* (contra Carrano et al., 2002), and *Eoraptor* (contra Carrano et al., 2002) (Fig. 81A). The same weak development of the ischial antitrochanter is present in many tetanuran theropods (Fig. 81B).

The ischial antitrochanter is very strongly developed in coelophysoids, *Ceratosaurus*, and *Carnotaurus*. The surface of the iliac antitrochanter faces ventrolaterally, whereas the ischial antitrochanter faces dorsolaterally. The two surfaces meet at a sharp angle along the ilium-ischium contact. The ischial antitrochanter projects from the iliac peduncle of the ischium far into the acetabular cavity. This results in a pronounced lip that interrupts the continuity of the acetabular border, and forms what was described as a 'notch' in the posteroventral rim of the acetabulum (Fig. 81C).

The derived state is coded as present in *Dilophosaurus*. There is a large antitrochanter on each of the proximal ischia of the holotype (UCMP 37302), but it does not protrude into the acetabulum as much as in other coelophysoids (Fig. 81D). There may be an ontogenetic component to the size of this structure, and given the early ontogenetic stage of the holotype (juvenile, see Chapter 1) there is the possibility the ischial antitrochanter would be considerably larger in more mature individuals.

215. Proximal plate of ischium solid or with fully enclosed ischial foramen (0), or ischial foramen ventrally open, cutting off obturator process from anterior process of ischium (1) (modified from Rauhut, 2003).

The transformation of the obturator process through theropod phylogeny was detailed by Hutchinson (2001a), and will not be entirely revisited here. In brief, the ischial portion of the puboischiadic plate underwent reduction much in the same manner as the pubis. First, perforation of the ischial plate and obturator process created an ischial foramen, as preserved in taxa such as *Segisaurus* and the basal tetanurans *Monolophosaurus* and *Yangchuanosaurus* (Molnar et al., 1990; Zhao and Currie, 1993). Continued increase in the size of the pelvic fenestra through the evolutionary history of theropods eventually breached the border of the ischial foramen, opening its ventral border. This isolated the posterior part of the obturator process from the rest of the anterior process of the ischium. This feature is present only in *Allosaurus* and *Ornitholestes* among the tetanurans included in this study.

216. Obturator process of ischium continuous with ischial shaft (0), or distally separated from ischial shaft by notch (1) (Rauhut, 1995; Carrano et al., 2002).

The ischial portion of the puboischiadic plate, including the obturator process, is continuous from the pubic contact to between the ischial shafts in *Marasuchus*, *Herrerasaurus*, and basal sauropodomorphs (Fig. 81A). In contrast, a number of relatively basal theropods have a distinct notch separating the posteroventral end of the obturator process from the ischial shaft. Taxa in my analysis that unambiguously preserve this feature include *Dilophosaurus* (Fig. 81D), adequately preserved and prepared specimens of *Coelophysis* (MCZ 4330), *Syntarsus rhodesiensis* (QG 1, QG 691) *Ceratosaurus* (USNM 4375), *Carnotaurus* (MACN-CH 894), and *Allosaurus* (Fig. 81B).

The notch was coded as absent in *Coelophysis* and *Syntarsus* by Carrano et al. (2002). The notch is not present in *Elaphrosaurus*, *Torvosaurus*, *Baryonyx*, or *Ornitholestes*. The delicate ischial plate is not adequately preserved or exposed to assess the character in specimens of *Eoraptor*, *Liliensternus*, *Segisaurus*, and *"Syntarsus" kayentakatae*, and is left coded as missing data for these taxa.

217. Distal tip of ischium not anteroposteriorly enlarged (0), or enlarged ≤3 times (1), or >3 times (2) minimum anteroposterior width of ischial shaft (modified from Novas, 1993; Rauhut, 2003).

The distal end of the ischium terminates without enlargement in *Marasuchus*, *Herrerasaurus*, and the basal ornithischians *Lesothosaurus* and *Scutellosaurus* (Fig. 82A). There is a distal ischial expansion in basal sauropodomorphs, *Eoraptor*, most coelophysoids, *Elaphrosaurus*, *Ceratosaurus*, abelisaurids, and basal tetanurans. The distal expansion of the ischium is little more than a swelling that measures less than twice the minimum diameter of the ischial shaft in *Eoraptor*, basal sauropodomorphs, some coelophysoids, and *Torvosaurus* (Fig. 82B). The distal expansion of the ischial shaft is markedly larger in *Dilophosaurus* (TMM 43646-26, 43646-33), *Elaphrosaurus*, *Ceratosaurus*, and *Carnotaurus*, its anteroposterior width measuring at least three times the minimum anteroposterior diameter of the ischial shaft (Fig. 82C, D). The term 'ischial boot' or 'foot' has been applied to the extra-large distal expansion in these and other taxa (Holtz, 1998; Rauhut, 2003).

218. Femoral head oriented anteromedially (0), or strictly medially (1) when distal condyles set perpendicular to axial column (Novas, 1991; Holtz, 1994).

The femoral head of most basal dinosaurs is directed anteromedially between 20 and 45 degrees from an axis through the acetabulae. The primitive condition is retained in *Marasuchus*, *Herrerasaurus*, *Lesothosaurus*, *Scutellosaurus*, *Plateosaurus*, *Eoraptor*, coelophysoids, and abelisaurs. The femoral head is reoriented in the tetanuran lineage, so that it projects medially instead of mediolaterally. The evolution of this transformation was recently described by Hutchinson (2001b).

This character was written in a multitstate format by Carrano et al. (2002). They recognized three degrees of femoral head orientation: 45 degrees anteromedial, 20-35 degrees anteromedial, and directly medial. Most of the taxa shared between their analysis and my study are scored congruently, with the exception of *Torvosaurus* and *Eustreptospondylus*. No femoral elements referable to *Torvosaurus* have ever been described. Unless Carrano et al. (2002) were privy to unpublished specimens or information there is no way this character could be evaluated for the taxon. The character is coded as missing data for *Torvosaurus*. *Eustreptospondylys* was scored with a femoral head oriented between 20 and 35 degrees by Carrano et al. (2002), but then scored with a medially directed femoral head by Rauhut (2003). I follow the latter assessment here.

219. Femoral head directed slightly ventrally (0), or horizontally or slightly dorsally (1) (Harris, 1998; Tykoski, 1998).

The femoral head angles ventrally in *Marasuchus*, *Herrerasaurus*, *Lesothosaurus*, *Plateosaurus*, *Eoraptor*, coelophysoids, *Elaphrosaurus*, *Ceratosaurus*, and abelisauroids. It is directed horizontally, at approximately the same level as the greater trochanter in spinosaurids, *Eustreptospondylus*, *Allosaurus*, and *Ornitholestes*. *Torvosaurus* was scored as having this character (Carrano et al., 2002), but no femoral pieces are described or published for this taxon. I leave the character scored as missing data for the taxon.

220. Femoral head relatively continuous with posterior surface of femur (0), or set off by well defined oblique ligament groove on posterior surface, giving 'hooked' proximal profile to femoral head (1) (Rauhut, 2003).

The posterior surface of the proximal femur of basal dinosauriforms (e.g., *Marasuchus*), *Herrerasaurus*, *Lesothosaurus*, and basal sauropodomorphs bears no sulci or grooves that distinctly set the femoral head off from the posterior surface of the femur. *Eoraptor* and almost all more derived theropods bear a distinct sulcus on the posterior surface that runs proximedially to distolaterally across the femoral neck (Fig. 83A, B). The sulcus is accentuated in many taxa by a posterior and posteroventral lip on the edge of femoral head that cups the sulcus medially. The profile of the femur's proximal end has a posterior 'hook' to it formed by the curled over posterior lip of the femoral head and the posterior sulcus adjacent to it (Fig. 83B).

This character was scored as absent in Abelisauridae by Rauhut (2003), based upon its apparent absence in *Carnotaurus* (Bonaparte et al., 1990:fig.32C). The posterior sulcus is present in the abelisauroid *Masiakasaurus* (Carrano et al., 2002), and in the

purported abelisaurid *Xenotarsosaurus* (TMM 45591-1, cast of holotype femur UNPSJB Pv. 612) (Fig. 83C). The morphology of the proximal femur was not described in the preliminary description of *Aucasaurus* (Coria et al., 2002), and I leave the character scored as missing data for the taxon.

221. Femoral dimorphism not present (0), or present, expressed in muscle scars, attachments, and processes ('robust' versus 'gracile' morphs) (1) (Rowe and Gauthier, 1990).

The apparent dimorphism in the skeleton of some coelophysoid taxa was acknowledged by several authors (Raath, 1977, 1990; Colbert, 1989, 1990; Rowe and Gauthier, 1990; Rowe et al., 1997; Tykoski, 1997, 1998). Bimodal distributions were documented in several skeletal components, including proportional differences in the head, neck, and forelimb, as well as size of muscular processes of the ulna, and femur (Raath, 1977, 1990). The noticeable dimorphism in the femur was most often cited by workers and used as a phylogenetic character.

The dimorphism expressed in the femur of some coelophysoid taxa manifests itself in the relative degree of muscle scarring and development of muscular attachments. The greater trochanter, scars on the proximal end of the femur, shape of the anterior trochanter, and presence or absence of the trochanteric shelf are the most obvious sites of dimorphic variation in the coelophysoid femur (Fig. 84A, B). The anterior surface of the distal femur and the medial epicondyle may also be sites of dimorphic expression, but the possibility was not thoroughly explored in the available samples. The structure of the

anterior trochanter and trochanteric shelf may also provide phylogenetic information and are discussed below.

Only taxa represented by multiple individuals of approximately the same ontogenetic stage can be evaluated for this character. Most of the fossil theropods included in this analysis, and most fossil theropods in general, are known from specimens representing a single or very few individuals. Dimorphic taxa may only express their bimodal morphologies in relatively mature individuals. This requires the character be evaluated only in those taxa known from multiple individuals that reached a minimum ontogenetic stage of development, in the case of coelophysoids the sub-adult stage. The derived state is scored as absent in a taxon if at least five individuals of at least sub-adult stage are known, and they all lack the structure of interest. The derived state is scored as present if two individuals of at least sub-adult stage are present and each preserves a different femoral morphology.

Femoral dimorphism is present in *Coelophysis* (Colbert, 1989, 1990), *Syntarsus rhodesiensis* (Raath, 1977, 1990), the Shake-N-Bake taxon (Tykoski, 1997, 1998), *Ceratosaurus* (Britt et al., 2000), and *Masiakasaurus* (Carrano et al., 2002). Partial to complete femora are known from at least five individuals of *"Syntarsus" kayentakatae* (MNA V2623 type and paratypes, TMM 43688-1, UCMP 128659) and all but UCMP 128659 exhibit robust morphology (Fig. 84C). The character cannot be reliably coded as present for *"Syntarsus" kayentakatae* though, because there is too great an ontogenetic difference between specimen UCMP 128659 and the next more mature specimen (TMM 43688-1). If expression of dimorphism was controlled by the onset of sexual maturity as

speculated (Raath, 1977, 1990), then the gracile condition in the UCMP femur could be the result of the immaturity of the individual. This character is coded as missing data for the taxon.

Dilophosaurus is known mostly from a handful of ontogenetically immature specimens that bear a gracile femoral morphology (Fig. 84D). The single known adult *Dilophosaurus* specimen (UCMP 77270 - see Chapter 1) has a robust femoral morphology. The expression of robust morphology in this specimen is probably not a simple matter of maturity. A proximal femur referred to *Dilophosaurus* (TMM 43662-2) is from an individual of comparable size to UCMP 77270, but it exhibits the gracile structure of the anterior trochanter and trochanteric shelf. This specimen (TMM 43662-2) was also an adult given its size, and therefore femoral dimorphism was probably present in *Dilophosaurus*.

222. Femoral anterior trochanter a low ridge or tuberosity (0), or a conical spike or pyramidal prominence (1), or a mediolaterally compressed flange (=aliform process) projecting anteriorly from femur (2) (modified from Gauthier, 1986; Carrano, 2000). (UO)

The term 'anterior trochanter' is used throughout this work in reference to the tubercle or process located on the anterior or anterolateral surface of the dinosaurian femur, proximal to the trochanteric shelf and its homologues. The nomenclature for this structure is divided among paleontologists. It has been labeled the 'lesser trochanter' (Gilmore, 1920; Janensch, 1925; Romer, 1956; Madsen, 1976; Raath, 1977; Padian,

1986; Colbert, 1989; Bonaparte et al., 1990; Currie and Zhao, 1993; Holtz, 1994; Hutchinson, 2001b; Carrano et al., 2002; Brochu, 2003; Rauhut, 2003), the 'anterior trochanter' (Welles, 1984; Gauthier, 1986; Rowe, 1989; Novas, 1992, 1993, 1996; Sereno et al., 1994; Sereno et al., 1996; Rowe et al., 1997; Holtz, 1998; Sereno, 1999a; Madsen and Welles, 2000), and most recently the 'cranial trochanter' (Weishampel et al., 2004).

Romer (1956) referred to this tuberosity in dinosaurs as the lesser trochanter, but admitted that it was not homologous to the process of the same name present in mammals and other synapsids. A recent study (Hutchinson, 2001b) hypothesized that the anterior (=lesser) trochanter was merely an anterior expansion of the trochanteric shelf. It was also opined that the trochanteric shelf originated within Dinosauromorpha, further evidence that the archosaurian trochanter is not homologous to the mammalian lesser trochanter (Hutchinson, 2001b). The lack of homology between the archosaurian and mammalian 'lesser' trochanters argues against sharing the term between these taxa. I restrict the term 'lesser trochanter' to the mammalian/synapsid feature, and use the term 'anterior trochanter' in reference to the structure in dinosauromorph archosaurs.

The anterior trochanter is highly variable in its size, degree of development, and relative position among dinosauromorphs. It is no more than a small raised ridge in basal dinosauriforms such as *Marasuchus*, as well as in *Herrerasaurus* and the basal sauropodomorph *Saturnalia* (Novas, 1993; Sereno and Arcucci, 1994; Langer, 2003). It is only a longitudinal rugosity on the femur of *Plateosaurus* and most other basal sauropodomorphs (Galton and Upchurch, 2004).

There was an abrupt change in the prominence of the anterior trochanter in some ornithischians and theropods. It is very strongly developed into an anteroposteriorly oriented and mediolaterally compressed flange in the relatively basal ornithischians *Lesothosaurus*, *Scutellosaurus*, and in ornithopods. The anterior trochanter protrudes sharply from the anterior surface of the femoral shaft in all theropods more derived than *Eoraptor*. The trochanter's morphology in *Eoraptor* is uncertain because of the preservational quality of the specimen. The form of the anterior trochanter varies between coelophysoids, other non-tetanuran theropods, and tetanurans.

The anterior trochanter (exclusive of the trochanteric shelf) is massive in robust individuals of many coelophysoid taxa. The anterior trochanter is triangular to subpyramidal in these taxa, and has a very rugose texture (Fig. 84B, C). The trochanter is relatively broad at its base and tapers sharply to the proximal tip. It juts from the body of the femoral shaft and is not separated from it by a cleft or other abrupt division. The broadest surface of the trochanter faces anterolaterally when the distal femoral condyles are oriented normal to the vertebral column. Taxa for which this morphology is unambiguously present include *Dilophosaurus* (UCMP 77270), *"Syntarsus" kayentakatae* (MNA V2623, TMM 43688-1), *Segisaurus* (UCMP 32101), *Coelophysis* (AMNH 7223, 7224, TMM 45559-7, many others), *Syntarsus rhodesiensis* (QG1, many others), and the Shake-N-Bake taxon (MCZ 9445, TMM 43689-16, many others).

A dramatic change occurred to the anterior trochanter in Ornithischia and within Theropoda. The anterior trochanter transformed from a small tuberosity to a mediolaterally compressed, flange-like process. Previous workers reffered to this

morphology as 'wing-like' or 'aliform' (Gauthier, 1986; Holtz, 1994). *Lesothosaurus* and *Scutellosaurus* both bear a large flange-like anterior trochanter that is expanded proximally to the level of the femur's proximal surface. The trochanter is oriented so it is nearly perpendicular to the femoral surface from which it projects.

Most fossil theropods also have a mediolaterally narrow anterior trochanter that projects anteriorly and proximally from the femoral shaft. The posterior edge of the flange is separated from the femoral shaft and greater trochanter by a deep cleft. Most previous workers considered an 'aliform' anterior trochanter only present in tetanuran theropods (Gauthier, 1986; Holtz, 1994, 1998; Sereno, 1999; Carrano et al., 2002; Rauhut, 2003). The anterior trochanter is also flange-like in *Ceratosaurus*, *Elaphrosaurus*, *Masiakasaurus*, and abelisaurids (Gilmore, 1920; Janensch, 1925; Carrano et al., 2002) (Fig. 85A). The major difference between the trochanters in these taxa and tetanurans is the relatively smaller size in the non-tetanuran taxa. It may not reach a level proximally beyond the mid-point of the femoral head, even with the slight declination of the femoral head in these taxa. The difference in anterior trochanter size between non-tetanurans and tetanurans is addressed as a separate character in my analysis.

Coelophysoids present difficulties for assessing this trochanteric morphology. Previous works scored this state absent in coelophysoids (Gauthier, 1986; Holtz, 1994, 1998; Carrano et al, 2002; Rauhut, 2003), and there is no question the anterior trochanter of robust individuals is not flange-like. The trochanters on most specimens of *Dilophosaurus* (UCMP 37302, TMM 43662-2) and *Liliensternus* (Huene, 1934; Rauhut,

2003:fig 42A) are subconical spikes that project proximally and slightly anteromedially from the femoral shaft. The anterior trochanter on the femur of at least one *Dilophosaurus* specimen (UCMP 37302) is somewhat narrower mediolaterally than anteroposteriorly (Fig. 84D), but it cannot be described as a 'wing' or 'flange'. The same condition is present on the femur of an immature specimen referred to *"Syntarsus" kayentakatae* (UCMP 128659).

The anterior trochanter in gracile individuals of *Syntarsus rhodesiensis* and the Shake-N-Bake taxon is flange-like and resembles the non-tetanuran taxa mentioned above that were coded as possessing a mediolaterally compressed, 'wing-like' anterior trochanter (Fig. 85B). The trochanter is positioned low on the proximal femur and barely reaches proximally to the level of the femoral head. The anterior trochanter angles anteriorly when the distal femoral condyles are set perpendicular to the vertebral column (Fig. 85C). The flange of the anterior trochanter is set off from the femoral shaft by a distinct cleft, just as in taxa such as *Ceratosaurus*, *Xenotarsosaurus*, and *Masiakasaurus* (Gilmore, 1920; Martinez et al., 1986; Carrano et al., 2002). Another juvenile individual of *Dilophosaurus* also has flattened, flange-like anterior trochanters on its femora (TMM 43646-61, 43646-74). I have not been able to examine a large sample of *Coelophysis* to see if the trochanter in gracile individuals of this taxon is subconical or flange-like. The derived character state is present in *Syntarsus rhodesiensis* and the Shake-N-Bake taxon. It is scored as missing data in *Dilophosaurus* and *Lilientsternus* because of the lack of unequivocally mature, gracile individuals. The character is also scored as missing data in *Coelophysis*, *Segisaurus*, and *"Syntarsus" kayentakatae*, because gracile individuals of

the taxon were not examined, or there are no unequivocal gracile adult individuals represented by known specimens.

223. Femoral anterior trochanter does not reach proximally to mid-point of femoral head (0), or reaches proximally at least to mid-point of femoral head (1) (modified from Gauthier, 1986).

The position of the proximal tip of the anterior trochanter relative to the femoral head was frequently used in cladistic analyses of theropod relationships (Holtz, 1994; 1998; Carrano et al., 2002; Rauhut, 2003). The anterior trochanter reaches the level of the distal edge of the femoral head in *Marasuchus*, *Herrerasaurus*, and coelophysoids (Figs. 84A-D). This contradicts statements and scoring in analyses that the anterior trochanter is positioned completely below (i.e. distal) to the femoral head in coelophysoids (Rauhut, 2003). The anterior trochanter also reaches the level of the femoral head in *Ceratosaurus*, *Elaphrosaurus*, *Carnotaurus*, and *Xenotarsosaurus* (Fig. 85A), but does not reach proximally to the level of the middle of the femoral head. The anterior trochanter extends much more proximally in most tetanurans theropods, reaching at least to the level of the middle of the femoral head.

224. Femoral trochanteric shelf large and pronounced (0), or expressed as low mound or swelling distolateral to anterior trochanter (1) in adults (modified from Carrano et al., 2002).

The trochanteric shelf (Andrews, 1921) is a prominent ridge that starts on the anterior surface of the proximal femur and continues laterally and distally around the femoral shaft (Fig. 84B, C). Hypotheses of its muscular attachments were recently covered by Hutchinson (2001b), who determined that the structure probably represents the site of the M. iliofemoralis insertion. The presence of a pronounced trochanteric shelf on the proximal femur was cited as a synapomorphy of Ceratosauria by Gauthier (1986), and Rowe and Gauthier (1990). However, a strong trochanteric shelf is also present on the femur in *Marasuchus* (Sereno and Arcucci, 1994), *Pseudolagosuchus* (Novas, 1996), *Herrerasaurus* (Novas, 1993), the basal sauropodomorph *Saturnalia* (Langer et al., 1999; Langer, 2003), and the probable dinosauriform *Silesaurus opolensis* (Dzik, 2003). There is no trochanteric shelf in the holotype of *Eoraptor*. The trochanteric shelf appeared at least at the level of Dinosauriformes, and its presence in several coelophysoids, *Ceratosaurus*, and *Xenotarsosaurus* may simply be retention of a plesiomorphic condition for Dinosauria. The trochanteric shelf is absent in basal ornithischians, and in sauropodomorphs more derived than *Saturnalia*.

It is also possible that the trochanteric shelf is only expressed in relatively mature individuals of those taxa that retain the feature. This may explain its absence in the holotype of *Eoraptor*. Juvenile specimens of *Dilophosaurus*, *Syntarsus rhodesiensis*, *Liliensternus* (see Chapter 1), and very small specimens of the Shake-N-Bake taxon do not bear a trochanteric shelf on the femur. The absence of the trochanteric shelf in some coelophysoids can only be reliably determined in those taxa represented by multiple examples of mature individuals. Because of this, the character (trochanteric shelf

represented only by a low mound or swelling) is scored as missing data in *Liliensternus*, *Segisaurus*, and *"Syntarsus" kayentakatae*. The latter two taxa are coded this way because the only relatively mature specimens known for each (one sub-adult specimen of *Segisaurus*, one sub-adult and one reasonably complete adult of *"Syntarsus" kayentakatae*) are all robust individuals with a pronounced trochanteric shelf. The character is coded as missing data in *Coelophysis* because published descriptions of the variation in the taxon's femur are insufficient to determine the distribution of the morphology with certainty, and I did not have the opportunity to evaluate a large number of *Coelophysis* femora prior to this work.

The trochanteric shelf is dramatically reduced in size and prominence in a number of abelisauroids (e.g., *Elaphrosaurus*, *Carnotaurus*, *Masiakasaurus*) and all adequately preserved tetanurans known to date. Only a low swelling with some textural difference from the adjacent femoral shaft marks the ancestral position of the trochanteric shelf in these taxa. The trochanteric shelf is also a mound-like swelling in mature, gracile individuals of some coelophysoid taxa, including at least *Dilophosaurus* (TMM 43662-2), *Syntarsus rhodesiensis*, and the Shake-N-Bake taxon (Figs. 84A, 85B). The character is coded as present in these taxa. The intention here is to let character distribution illustrate the evolution of the trochanteric shelf. It should determine whether the trochanteric shelf is truly plesiomorphic for Theropoda and its reduction is unique to abelisauroids and Tetanurae, or whether the reduction of the trochanteric shelf actually occurred at the base of Theropoda and its retention is unique to coelophysoids, *Ceratosaurus*, and *Xenotarsosaurus*.

225. Medial epicondyle of femur weak (0), or strongly developed ridge (1), or hypertophied and flange-like (2) (Forster, 1999).

The anteromedial edge of the distal femur is smoothly rounded in basal dinosauriforms, ornithischians, and sauropodomorphs, and *Herrerasaurus*. The anteromedial edge of the distal femur is difficult to see in the available cast of the holotype of *Eoraptor*, and the character is left scored as missing data for the taxon. The anteromedial edge of the distal femur is drawn out medially as a ridge in other theropods, forming a pronounced medial epicondyle (Fig. 86A, B). The abelisauroids *Masiakasaurus*, *Xenotarsosaurus*, and *Carnotarus* take the development of the medial epicondyle further, resulting in an enlarged medial flange on the distal femur (Martinez et al., 1986; Bonaparte et al., 1990; Carrano et al., 2002) (Fig. 86C, D). It is possible, if not probable that the expression of an expanded medial epicondyle occurs only later in ontogeny. The character should be appraised only in taxa represented by ontogenetically advanced individuals (see Chapter 1).

The primitive state of this character was coded for *Liliensternus* and *Dilophosaurus*, but a derived state was considered present in *Coelophysis* and *Syntarsus* by Carrano et al. (2002). The character is coded as missing data for *Liliensternus*, given the results of the ontogenetic analysis in Chapter 1. The right femur of UCMP 77270 (*Dilophosaurus*) preserves an enlarged, ridge-like medial epicondyle. It is similar in size and proximal-ward extent to those of the holotype (MNA V2623) and referred (TMM

43688-1) specimens of *"Syntarsus" kayentakatae*. Derived state "1" is coded for *Dilophosaurus*.

226. Anterior surface of femoral distal end flat or convex (0), or with broad, shallow, depression bordered medially by medial epicondyle (1) in adults (Rauhut, 2003).

227. Tibiofibular crest of femur smoothly continuous with lateral distal condyle (0), or sharply demarcated from lateral distal condyle by sulcus or concavity (1) (Rowe, 1989).

The tibiofibular crest (=crista tibiofibularis sensu Baumel and Witmer, 1993) was misidentified by Rauhut (2003:164) in his criticsm of the characters originally put forth as diagnostic of Ceratosauria by Rowe and Gauthier (1990). The term was incorrectly applied to an oblique ridge on the medial surface of the proximal fibula of some coelophysoid taxa. The tibiofibular crest is a protuberance on the posterior surface of the distal femur (Fig. 87A-C). It is located proximal and medial to the lateral (=fibular) condyle. It slots between the proximal ends of the tibia and fibula during flexion of the lower hindlimb in extant Theropoda, and presumably did the same in extinct forms. The structure has had many names applied to it including ectocondylar tuber (Welles, 1984; Charig and Milner, 1997), external tibial condyle (Martínez et al., 1986), tuberous process of the femur (Madsen and Welles, 2000), and crista tibiofibularis (Rowe, 1989; Baumel and Witmer, 1993).

The tibiofibular crest is smoothly continuous with the lateral condyle of the distal femur in most dinosauriform taxa. It was noted by Welles (1984) that the base of the crista tibiofibularis bore a deep lateral sulcus in *Dilophosaurus* (Fig. 87A). A similar groove was described by Rowe (1989) in the femur of *"Syntarsus" kayentakatae* (Fig. 87B), and its presence was considered a synapomorphy of Ceratosauria. The lateral sulcus on the tibiofibular crest is also present in specimens of the Shake-N-Bake taxon and *Coelophysis* (TMM 45559-12, TMM 45559-15) (Fig. 87C). It is not present on the femur of the most immature individual of *Dilophosaurus* known to date (TMM 43646-61). It is not present in UCMP 128659, a juvenile individual probably referable to *"Syntarsus" kayentakatae*, or in a sub-adult *"Syntarsus" kayentakatae* specimen (TMM 46388-1). It is possible that the sulcus is another feature expressed only in later stages of ontogeny.

The tibiofibular crest is sharply separated from the lateral condyle in *Ceratosaurus* and *Masiakasaurus* (Gilmore, 1920; Carrano et al., 2002). This character was scored as present in *Carnotaurus* by Carrano et al. (2002) and I follow that assessment here. The distal femur of *Xenotarsosaurus* (TMM 45591-1; cast of holotype femur) has a deep concavity on the lateral surface of the tibiofibular crest. It is broader than the narrow groove present in the other taxa mentioned above, but it still serves to abruptly divide the crest from the lateral condyle of the femur. This character was scored as absent for *Xenotarsosaurus* by Carrano et al. (2002), but is coded as present here.

228. Femoral popliteal fossa smooth (0), or traversed by infrapopliteal ridge between medial (=tibial) distal condyle and tibiofibular crest (1) in adults (Tykoski 1998).

The popliteal fossa (=intercondylar groove of Carrano et al., 2002) of almost all dinosauriforms is an uninterrupted longitudinal groove on the posterior surface of the distal femur (Fig. 88A). The fossa is divided into more proximal and distal parts by a low ridge in several theropods, including *"Syntarsus" kayentakatae* (Fig. 88B), *Coelophysis* (TMM 45559-12, TMM 45559-15), the Shake-N-Bake taxon (TMM 43689-7), *Ceratosaurus* (Gilmore, 1920; Madsen and Welles, 2000), *Xenotarsosaurus* (TMM 45591-1) (Fig. 88C), and *Carnotaurus* (Bonaparte et al., 1990). The infrapopliteal ridge may correspond to an area of attachment for the cruciate ligaments. There is no evidence for an infrapopliteal ridge in specimens of *Liliensternus* and *Dilophosaurus*, although the area of the popliteal fossa is not well preserved in UCMP 77270, the only adult *Dilophosaurus* individual known. No ridge is present within the popliteal groove on the femur of *Masiakasaurus* (Carrano et al., 2002), nor is it present in basal tetanurans.

229. Anteroposterior length of cnemial crest of tibia < (0), or ≥ (1) width across proximal (=femoral) condyles of tibia.

The cnemial crest of the tibia is relatively small in sauropodomorphs, *Herrerasaurus*, and *Marasuchus* (Novas, 1993; Sereno and Arcucci, 1994) (Fig. 89A). It is pronounced in more derived theropods, protruding further anteriorly and bearing a more laterally 'hooked' profile (Fig. 89B). The anteroposterior width of the cnemial crest in most theropod taxa remains less than the greatest mediolateral breadth across the

proximal articular condyles of the tibia. The cnemial crest is greatly enlarged in several ceratosaur taxa, including *Ceratosaurus*, *Xenotarsosaurus*, *Aucasaurus*, and *Masiakasaurus* (Gilmore, 1920; Martinez et al., 1986; Coria et al., 2002; Carrano et al., 2002) (Fig. 89C). The anteroposterior dimension of the cnemial crest in these taxa exceeds the mediolateral width of the proximal tibial condyles. It is very likely that the same condition was present in the tibia of *Carnotaurus*, but the anterior part of the cnemial crest is not preserved in the only known specimen, making accurate measurements impossible.

230. Lateral surface of cnemial crest of tibia flat (0), or excavated by longitudinal fossa, giving tibia laterally 'hooked' profile in proximal view (1) (modified from Sampson et al., 1998).

231. Proximal condyles of tibia continuous (0), or separated by cleft along posterior rim of tibia in proximal view (1) (Rauhut, 2003).

232. Anterior tip of cnemial crest of tibia not expanded (0), or proximodistally expanded (1) (Forster, 1999).

The cnemial crest of the tibia of most theropods tapers anteriorly to create an approximately triangular profile to the proximal tibia in lateral or medial view (Fig. 90A). The cnemial crest of most neoceratosaurs is anteroposteriorly longer than is typical of theropods, but the anterior edge of the crest is dramatically enlarged in some

abelisauroids. The cnemial crest of *Ceratosaurus* (Fig. 90B) is slightly larger in the proximodistal direction than those of coelophysoids and tetanurans, and the abelisauroids *Masiakasaurus* (Fig. 90C) and *Xenotarsosaurus,* but the crest does not bear a substantial expansion at the anterior tip. In *Majungatholus* and *Aucasaurus* the cnemial crest is enlarged proximodistally to the extent that the crest appears subrectangular in medial and lateral view (Fig. 90D, E). I score this character present in *Majungatholus* and *Aucasaurus*, but absent in *Masiakasaurus*, *Xenotarsosaurus*, *Ceratosaurus*, *Elaphrosaurus*, coelophysoids and tetanurans. This differs dramatically from the scoring of this character by Carrano et al. (2002), who considered it present in all the neoceratosaurs listed above (plus *Carnotaurus*) except *Elaphrosaurus*. Also, this character cannot be confidently assessed in *Carnotaurus* because the anterior margin of the cnemial crest was not preserved (Bonaparte et al., 1990).

233. Fibular crest (=crista fibularis) of tibia absent (0), or low ridge extending distally from proximal tibia (1), or distally placed, flange-like, separated from proximal tibia (2) (Gauthier, 1986; Perez-Moreno et al., 1993; Rauhut, 2003).

The presence of a fibular crest (=crista fibularis) on the lateral surface of the proximal tibia was first used in a character-based analysis by Gauthier (1986). It is absent in *Marasuchus*, ornithischians, basal sauropodomorphs, and *Herrerasaurus*. The fibular crest was coded as absent in *Eoraptor* by Rauhut (2003). The lateral surface of the proximal tibia is not visible in the cast of the *Eoraptor* holotype skeleton (TMM 43451-2) exmained for this work, and character is coded as missing data in *Eoraptor*.

234. Tibia and fibula spaced apart (0), or closely appressed (1) through most of shafts' length (Gauthier, 1986; Holtz, 1994).

235. Distal end of tibia anteriorly flat or weakly convex (0), or with broad anterior fossa bearing oblique (proximolateral to distomedial) proximal border (1) (modification of Rauhut, 2003).

This character is re-worded here to reflect a change in emphasis compared to its original form (Rauhut, 2003). Previously, the character focused upon the robustness of the dorsal margin of the distal tibia's anterior fossa. This generated the impression that the buttress forming the dorsal margin of the fossa was the central point acted upon during the evolution of the theropod distal tibia. The relative size of the fossa's dorsal rim should instead be viewed as an after-effect of the change in position and size of the tibia's distal fossa.

The distal fossa on the anterior surface of the dinosaurian tibia receives the ascending process of the astragalus. The articulation between the tibia and the ascending process of the astragalus is positioned on the laterodistal surface of the tibia in taxa such as *Marasuchus*, *Herrerasaurus*, basal sauropodomorphs, and *Eoraptor* (Fig. 91A, B). The tibia functionally rests atop the ascending process in these taxa, with a large part of the articular facet for the astragalus and ascending process facing distally or laterodistally. As much as half of the tibia's anteroposterior girth may be positioned anterior to a transverse plane through the ascending process of the astragalus.

The tibia's fossa for articulation with the ascending process of the astragalus and the ascending process itself are both shifted to the anterior margin of each bone in more derived theropods (Fig. 91C, D). This reduced the relative proportion of the tibia's shaft that was positioned anterior to a transverse plane through the ascending process of the astragalus. The oblique buttress or ridge on the anterior surface of the tibia is not an evolutionary novelty. It is simply the distal edge of the shaft of the tibia that remains anterior to the ascending process and the articular fossa for it on the tibia. The form of the anterior fossa continued to change through the evolution of Theropoda. The fossa became even shallower and less distinct in many tetanuran taxa. This reflected the continued anterior-ward shift of the ascending process of the astragalus, as well as the process' change from a wedge-like to laminar form.

236. Tibia distal profile subequant to subrectangular (0), or subrectangular with small posterolateral extension (1), or subtriangular with large posterolateral expansion (2) (modified from Gauthier, 1986; Sereno et al., 1994; Rauhut, 2003). (1). (O)

The distal profile of the tibia is subequant in *Marasuchus*, and *Herrerasaurus*, and subrectangular in basal ornithischians, basal sauropodomorphs, and *Eoraptor* (Fig. 91B). The distal tibia of *Eoraptor* bears a distinct posteroventral process that probably backed the ascending process of the astragalus, and may have reached posterior to the fibula (pers. obs. TMM 43451-2). In this regard the distal tibia of *Eoraptor* is more derived than that of *Herrerasaurus*, in which the posterventral process of the tibia does not protrude laterally to the fibula (Fig. 91B). The distal tibia in *Eorpator* is not as

mediolaterally expanded as in coelophysoid theropods, but the intermediate derived state of this character is coded as present in *Eoraptor* (contra Rauhut, 2003).

The distal tibia is noticeably wider mediolaterally than anteroposteriorly in all other theropods. The distal tibia has an almost rectangular distal profile in coelophysoids, but it bears a pronounced posterolateral extension that reaches laterally past the ascending process of the astragalus (Figs. 91B, C, 92A). The distal end of the coelophysoid tibia is hidden from view in intact adult specimens because of the fusion between the tibia and proximal tarsals common in the clade. The distal surface of the tibia is visible in immature individuals of *Dilophosaurus*, *Liliensternus*, and *Gojirasaurus*. It is not known if the relative proportions of the distal tibia changed through ontogeny in these taxa. Distal tibiotarsi of mature *"Syntarsus" kayentakatae* individuals (MNA V2623 paratype, TMM 43648-9) with broken or slightly disarticulated proximal tarsals are anteroposteriorly narrower in distal profile than the same elements in *Dilophosaurus* (TMM 43646-78, UCMP 77270) (Fig. 92A, B). The distal tibia is even more mediolaterally expanded relative to its anteroposterior width in *Elaphrosaurus*, *Ceratosaurus*, abelisauroids, and tetanurans (Fig. 92C). The posterolateral extension of the tibia is greatly enlarged in these taxa so that the tibia is approximately triangular in distal profile.

237. Medial side of proximal end of fibula flat (0), or excavated by longitudinal groove (1) (modified from Rowe, 1989; Rowe and Gauthier, 1990; Rauhut, 2003).

238. Medial side of proximal end of fibula flat (0), or with oblique (posteroproximal to anterodistal) ridge that overlaps proximal part of medial fibular groove (1) (Rowe, 1989; Rowe and Gauthier, 1990; Rauhut, 2003).

Some coelophysoid taxa bear a posterior-ward opening sulcus on the medial side of the proximal fibula, a feature listed as diagnostic of Ceratosauria by Rowe (1989) and Rowe and Gauthier (1990). The medial side of the fibula is excavated by a longitudinal groove or sulcus in a number of theropods. What is unique to several coelophysoids and perhaps also *Ceratosaurus* (USNM 4735, UUVP 56) is the presence of an oblique ridge that proximally caps the medial groove or sulcus in the fibula (Fig. 93). The ridge angles anterodistally from the posteroproximal corner of the fibula and disappears near the anterior margin of the fibula. The ridge is raised from the rest of the medial surface of the fibula and has a rough texture. It medially overlaps the proximal-most part of the longitudinal sulcus in the fibula, which probably resulted in early descriptions of the groove as opening posteriorly (Rowe, 1989; Rowe and Gauthier, 1990). The ridge on the medial surface of the proximal fibula was mistakenly identified as the crista tibiofibularis by Rauhut (2003).

The medial groove and oblique ridge near the proximal end of the fibula are reportedly absent in *Liliensternus*. They are both also absent from the immature specimens of *Dilophosaurus* (TMM 43646-61). Another *Dilophosaurus* specimen (UCMP 37302) bears only a weak medial groove on the proximal fibula. This led some previous workers to score the posterior-facing-groove character of Rowe (1989) as absent in *Dilophosaurus* (Rauhut, 2003). The proximal end of the badly weathered right fibula

of UCMP 77270 (*Dilophosaurus*) exhibits remnants of the oblique ridge. The presence of this structure in this adult specimen suggests the ridge may be expressed in later stages of ontogeny, which may also explain its absence in immature individuals such as TMM 43646-61, UCMP 37302, and in specimens of *Liliensternus*. The oblique ridge on the medial side of the proximal fibula is also present in *Segisaurus*, *"Syntarsus" kayentakatae*, *Coelophysis*, *Syntarsus rhodesiensis*, the Shake-N-Bake taxon, and *Ceratosaurus*. It is not present, or is not reported in abelisaurids and tetanurans.

239. Fibular M. iliofibularis insertion weak or indiscernible (0), or distinct small tubercle (1), or large anterolaterally projecting tubercule or process (2) (Rauhut, 2000; Carrano et al., 2002). (O)

240. Anteroposterior midshaft width of fibula >30% (0), or ≤ 30% (1) anteroposterior width of proximal end of fibula (Sereno, 1999a).

241. Fibula does not overlap astragalus (0), or bears medial flange that overlaps part of the ascending process of astragalus (1) (Rowe, 1989; Rowe and Gauthier, 1990).

The distal end of the fibula laterally contacts the ascending process of the astragalus in *Marasuchus*, basal sauropodomorphs, *Herrerasaurus*, and *Eoraptor*. The ascending process of the astragalus is positioned in a central location on the proximal surface of the astragalus, and the fibula is positioned entirely lateral to the ascending

process (Fig. 94A). A large fibular facet on the ascending process marks the contact between the two elements.

The fibula of some coelophysoids is derived in having an anteromedial flange on the distal end of the bone in adult specimens. This flange partially overlaps the ascending process of the astragalus in anterior view (Figs. 94B). There is no facet or visible contact surface on the anterior surface of the ascending process. The fibular flange is unquestionably present in adult specimens of *"Syntarsus" kayentakatae*, *Coelophysis*, *Syntarsus rhodesiensis*, and the Shake-N-Bake taxon. The fibular flange is not well developed in immature individuals of *Syntarsus rhodesiensis* (QG 768) (Raath, 1990:fig. 7.9A). As a result, the flange does not anteriorly overlap the ascending process of the astragalus in immature individuals. This also suggests that expression of this feature may be another maturity-dependent character.

There is no anteromedial flange on the distal fibula of *Liliensternus* (MB R. 2175) (Rauhut, 2003:fig. 55B), nor is there an overlapping flange on specimens of *Dilophosaurus* (UCMP 37302, 37303). An incipient anteromedial fibular flange was described on both of these *Dilophosaurus* specimens (Welles, 1984). The small anteromedial ridge on the fibula of UCMP 37302 butts against the ascending process of the astragalus, but does not anteriorly overlap it. UCMP 37303 preserves the left distal tibia, distal fibula, and proximal tarsals in articulation (Fig. 94C, D). The anteromedial edge of the distal fibula is broken and weathered, rendering the presence of the fibular flange uncertain in this individual. The distal fibula and proximal tarsals are not preserved in UCMP 77270. The fibulae known for *Liliensternus* and *Dilophosaurus* are

from immature individuals. The distal fibula and its relationship to the ascending process of the astragalus closely resemble that of immature specimens of *Syntarsus rhodesiensis*. It is possible the expression of this character is restricted to later stages of ontogeny, and as such should not be evaluated in taxa known only from immature individuals. The character is coded as missing data for *Liliensternus* and *Dilophosaurus*.

242. Fibula separate from (0), or co-ossifies with (1) ascending process of astragalus of adults (Carrano et al., 2002).

243. Fibular facet on proximal surface of astragalus large, intersects posterior rim of astragalus (0), or large, does not reach posterior rim of astragalus (1), or small subtriangular fossa on anterolateral corner of proximal surface of astragalus (2). (O)

The astragalus of dinosauriforms ancestrally bears a large fibular facet on the lateral part its proximal surface, a condition present in *Marasuchus*, *Herrerasaurus*, the ornithischian *Scutellosaurus*, and basal sauropodomorphs (Fig. 95A) (Novas, 1989b, 1993; Sereno and Arcucci, 1994). The proximal articular surfaces of the astragalus and calcaneum are not visibile in the available cast of *Eoraptor* (TMM 43451-2). The distal end of the fibula is quite large in the specimen, so it is likely the fibular facet on the astragalus corresponds in size. A large fibular facet is present on the astragalus of *Liliensternus* (listed by Rauhut [2003] as MB R. 2175) (Fig. 95B). It spans the anteroposterior breadth of the astragalus, reaching the posterior rim of the proximal

surface of the astragalus medial to the astragalus-calcaneum suture. This arrangement prevents the tibia from overlapping the posterior surface of the fibula.

The fibular facet on the astragalus is smaller in most other theropods. The reduction of the facet results from an increase in the size of the tibial facet on the astragalus, coupled with rotation of the planar long axis of the ascending process from an anteroposterior (Fig. 95A) to a posterolateral orientation. The posterolateral ridge from the ascending process intersects the lateral margin of the astragalus in most basal theropod taxa. The ridge excludes the fibular facet from the posterior rim of the astragalus, and facilitates the tibial contact and overlap of the posterior surface of the fibula.

The tibial facet of the astragalus is slightly expanded in the posterolateral direction in *Coelophysis*. The tibia barely reaches the posterolateral corner of the astragalus in TMM 45559-16, but the tibia in this specimen was broken and displaced laterally a small amount (Fig. 95C). The fibular facet of the astragalus is relatively long and narrow, but it is not clear if it reaches the posterior rim of the astragalus. Another *Coelophysis* specimen (CMNH 11894) has a tibia separated from the calacaneum by a short section of the rim of the astragalus, which leaves enough space for the posterior edge of the fibular facet of the astragalus (Fig. 95D). This resembles the condition in *Liliensternus*, and the primitive character state is coded as present for both taxa. Future examination of additional disarticulated proximal tarsals of *Coelophysis* may require changes in my evaluation of this character for the taxon.

The fibular facet is reduced in size in the astragalus of *Dilophosaurus* (UCMP 37302) (Fig. 96A), relative to that in *Liliensternus* and *Coelophysis*. The fibular facet is excluded from the posterior rim of the astragalus, and the posteroventral process of the tibia backs the fibular facet. The fibular facet on the astragalus is even more reduced in some other coelophysoids, *Ceratosaurus*, and tetanurans. The fibular facet is reduced to a small, subtriangular fossa on the anterolateral corner of the proximal surface of the astragalus (Fig. 96B). This morphology is present in the coelophysoids *"Syntarsus" kayentakatae* (TMM 43669-3), the Shake-N-Bake taxon (MCZ 9463), and *Syntarsus rhodesiensis* (QG 768, QG 816, others in Raath, 1977:pl. 25) (Fig. 96C).

244. Ascending process of astragalus height < (0), or ≥ (1) height of main body of astragalus (Carrano et al., 2002).

245. Ascending process of astragalus positioned near center of astragalus roximal surface (0), or near anteroproximal margin of astragalus (1).

The apex of the ascending process of the astragalus is positioned near the anteroposterior center of the proximal surface of the astragalus in theropod outgroups, *Herrerasaurus*, and *Eoraptor* (Fig. 95A) (Novas, 1989b, 1993). The apex of the ascending process is closer to the anterior edge of the astragalus in all more derived theropods, as well as in basal ornithischians (Figs. 95B, C, 96A-C). The anterior shift of the process also facilitated a shift in the relationship of the ascending process and the tibia.

246. Tibial facet of astragalus shallow and mostly medial to base of ascending process (0), or deep and extends posterior to base of ascending process (1) (Novas, 1989, 1996; Carrano et al., 2002).

The ascending process of the astragalus bears its contact with the tibia along its medial and proximedial surfaces in dinosauriforms ancestrally (Novas, 1989b, 1996). The axis of the process is anteroposteriorly oriented in basal taxa such as *Marasuchus*, and the process serves to widely separate the tibial and fibular articular facets on the proximal astragalus (Fig. 95A) (Sereno and Arcucci, 1994). The ascending process is anteroposteriorly abbreviated in *Herrerasaurus*, ornithischians, basal sauropodmorphs, and theropods (Novas 1989b, 1996). The distal tibia is expanded posterior to the ascending process in these taxa so that the tibial and fibular facets are separated by only a small posterior, or posterolateral ridge (Figs. 95B, 96A-C). The tibial facet on the ascending process is therefore located on the posterior side of the process.

The articulation of the tibia is further enhanced by the depth the tibia inserts into the proximal surface of the astragalus, as facilitated by a deep depression at the base of the ascending process (Novas, 1989b; 1996). This posterior fossa was described as present in Dinosauria ancestrally, although it is absent in the relatively basal ornithischian *Scutellosaurus* (Colbert, 1981; Novas, 1996). The fossa is present in *Herrerasaurus* (Novas, 1989b, 1996), basal sauropodomorphs (Cooper, 1981; Novas, 1989b), and all theropods more derived than *Eoraptor*. The proximal surface of the astragalus is difficult

to see in the available cast of *Eoraptor* (TMM 43451-2), and the posterior part of the better preserved astragalus and calcaneum is missing on the specimen.

This character was coded as absent in *Eoraptor*, *Herrerasaurus*, *Coelophysis*, *Syntarsus*, and *Liliensternus* by Carrano et al. (2002). I believe they interpreted the character differently than previous authors. There is a deep fossa posterior to the ascending process of the astragalus in specimens of *Coelophysis* (TMM 45559-16), *"Syntarsus" kayentakatae* (MNA V2623 paratype; TMM 43669-3), and *Syntarsus rhodesiensis* (QG 768). The posterior fossa in the astragalus of *Liliensternus* (Fig. 95B) is nearly as deep as it is in the type specimen of *Dilophosaurus*, a taxon for which this character was coded as being present by Carrano et al. (2002). I score this character present in all these coelophysoid taxa, in agreement with assessments by Novas (1989b, 1996).

247. Ascending process of astragalus robust, pyramidal prominence (0), or anteroposteriorly flattened (1) (Sereno et al., 1994).

248. Anterior surface of astragalus smooth, not grooved (0), or traversed by horizontal groove (1) (Gauthier, 1986).

It was long recognized that most basal tetanuran astragali bear a horizontal groove across the anterior surface of the element, halfway between the proximal and distal surfaces of the astragalus (Fig. 97A) (Welles and Long, 1974). The groove is deeply incised in many tetanuran taxa (e.g., *Torvosaurus*, *Sinraptor*), but is less sharply defined

in others (e.g., *Allosaurus*). Recent analyses recognized that some ceratosaurs also bear a horizontal sulcus across the anterior astragalar condyles (Carrano et al., 2002; Rauhut, 2003). These taxa include *Dilophosaurus*, *Elaphrosaurus*, *Ceratosaurus*, *Xenotarsosaurus*, *Majungatholus*, and *Masiakasaurus*. The two cited works disagreed with respect to the scoring of this character in *Dilophosaurus* and *Elaphrosaurus*. The horizontal groove was scored as present in *Dilophosaurus* and absent in *Elaphrosaurus* by Carrano et al. (2002), but just the reverse by Rauhut (2003).

The left astragalus of the *Dilophosaurus* specimen UCMP 37302 bears a deep groove in the anterior surface of the medial condyle, but the groove rapidly shallows to a faint sulcus toward the middle of the element (Fig. 97B). It is difficult to see given the preservation quality of the specimen. I therefore concur with the assessment of Carrano et al. (2002) and score the groove as present in *Dilophosaurus*. The condition in *Elaphrosaurus* is difficult to ascertain in photographs and illustrations of the left astragalocalcaneum. If an anterior groove is present on the astragalus, it is less deeply etched into the surface than in UCMP 37302. I leave this character coded as missing data for *Elaphrosaurus* because of the opposing opinions in previous works and my inability to establish its presence or absence from the literature.

A horizontal groove also crosses the anterior astragalus surface in several other coelophysoid taxa. This is a substantial departure from the previous understanding of the distribution of this feature. The groove is present in specimens of *Coelophysis* (TMM 45559-14, 45559-16) (Fig. 97C), *"Syntarsus" kayentakatae* (MNA V2623) (Fig94B), and the Shake-N-Bake taxon. The horizontal groove is expressed at least as well in these

specimens as in the tibiotarsus of *Masiakasaurus* (Carrano et al., 2002:fig. 16), and is more clearly defined than in the type of *Dilophosaurus* (UCMP 37302). It is not clear from descriptions or illustrations if a horizontal groove is present on the anterior surface of the astragalus of *Syntarsus rhodesiensis*, and the character is left coded as missing data for the taxon.

249. Astragalus and calcaneum remain separate (0), or fuse to each other (1) by adulthood (Rowe 1989).

This character and the next were omitted from some phylogenetic analyses of basal theropod relationships because of their variable expression in known specimens and obvious dependence upon the maturity level of a given individual (Carrano et al., 2002; Rauhut, 2003). Fusion between these elements is not present in outgroups to Theropoda, nor in basal tetanurans. The condition is present in some coelurosaurian clades, but these taxa are highly derived forms far removed from the basal Ceratosauria-Tetanurae divergence. They have little or no bearing on relationships at this early stage of theropod history. The fact that these co-ossifications occurred relatively early in the ontogenetic trajectory of coelophysoids and ceratosauroids, but not in more basal saurischians and basal tetanuran theropods, marks the conditions as potentially informative for phylogeny reconstruction.

The astragalus and calcaneum are separate elements in dinosauriformes ancestrally. They remain separate in adults of basal tetanuran taxa, including *Torvosaurus* and *Allosaurus* (Figs. 96B, 97A) (Gilmore, 1920; Madsen, 1976; Britt,

1991). An isolated calcaneum that shows no sign of fusion with the astragalus is known for *Baryonyx*, but the type specimen shows signs of immaturity and this character is only provisionally scored as absent in the taxon (Charig and Milner, 1997).

The astragalus and calcaneum are solidly co-ossified (forming an astragalocalcaneum) in most coelophysoids and ceratosauroids known from at least sub-adult individuals. Taxa that unequivocally possess the condition include *Camposaurus*, *Liliensternus* (Huene, 1934) (Fig. 95B), *Coelophysis* (Figs. 95D, 97C), *"Syntarsus" kayentakatae* (Fig. 94B), the Shake-N-Bake taxon, *Syntarsus rhodesiensis* (Raath, 1969, 1977, 1990), *Elaphrosaurus* (Janensch, 1925), *Ceratosaurus* (Gilmore, 1920; Madsen and Welles, 2000), *Xenotarsosaurus* (Martinez et al., 1986), *Aucasaurus* (Coria et al., 2002), *Majungatholus* (Samspon et al., 1998), and *Masiakasaurus* (Carrano et al., 2002). Fusion between these elements was coded as present in *Carnotaurus* by Carrano et al. (2002), but the proximal tarsals were not recovered with the type specimen (Bonaparte et al., 1990). This character is coded as missing data for *Carnotaurus*. The only proximal tarsals known for *Dilophosaurus* at this time came from immature individuals (UCMP 37302, UCMP 37303, TMM 43646-61). None of these specimens have signs of co-ossification between the astragalus and calcaneum (Figs. 94C, 96A, 97B). The character remains coded as missing data for *Dilophosaurus* because of the lack of a mature individual that preserves these elements.

250. Astragalus and tibia remain separate (0), or fuse to each other (1) by adulthood (Rowe, 1989).

This character is maturity-dependent in expression, but it does not share as widespread a distribution among coelophysoids and ceratosauroids. Fusion between the tibia and astragalus (resulting in a tibiotarsus) is present in *Camposaurus*, *Procompsognathus* (Sereno and Wild, 1992), *Coelophysis* (Fig. 98B), *"Syntarsus" kayentakatae* (Fig. 94B), the Shake-N-Bake taxon, *Syntarsus rhodesiensis* (Raath, 1969, 1977, 1990), *Ceratosaurus* (Gilmore, 1920; Madsen and Welles, 2000), *Xenotarsosaurus* (Martinez et al., 1986), *Aucasaurus* (Coria et al., 2002), and *Masiakasaurus* (Carrano et al., 2002). There is no sign of tibia-tarsal co-ossification in *Liliensternus*, but the known specimens are immature individuals. The character is coded as missing data for *Liliensternus* in my analysis. The one known adult specimen of *Dilophosaurus* (UCMP 77270) preserves a right tibia that shows no evidence of co-ossification with the proximal tarsals. I therefore code this character as absent in *Dilophosaurus*.

Coelophysis is highly variable with regard to the presence of tibia-tarsus fusion. It was correctly reported that some large, adult individuals (AMNH 7224) lack fusion between these elements, whereas some much smaller individuals (MNA V3318) have completely co-ossified tibiotarsi (Colbert, 1989, 1990). The variation in tibia-tarsus fusion is illustrated by CMNH 11894 and TMM 45559-14 (Fig. 98A, B). These two specimens come from individuals of approximately the same size and assumed ontogenetic stage. There is a clear suture separating the tibia and astragalocalcaneum in CMNH 11894, especially in posterior view (Fig. 98A). The tibia and astragalocalcaneum are solidly co-ossified to form a tibiotarsus in TMM 45559-14 (Fig. 98B). I have not yet examined a large sample of *Coelophysis* specimens, and can offer no explanation at this

time to account for the high degree of variation in tibia-tarsus co-ossification reported in the taxon (Colbert, 1989, 1990). Fusion between the tibia and astragalus is present in many individuals of the taxon, and because of this I code the condition as present in *Coelophysis*.

251. Calcaneum without tibial facet (0), or with small tibial facet on posteromedial corner (1), or with large tibial facet covering most of posterior surface and reaches nearly to lateral edge of calcaneum (2) (Sereno et al., 1996; Rauhut, 2003). (O)

The tibia is separated from the calcaneum by the ascending process of the astragalus in dinosauriforms ancestrally (e.g., *Marasuchus*) (Fig. 99A) (Sereno and Arcucci, 1994). The condition is present in much the same form in *Herrerasaurus* and basal sauropodomorphs (Novas, 1989b, 1993). The tibia broadly contacts the calcaneum in tetanurans, so much so that most of the posterior and posteromedial surface of the calcaneum is comprised of a large tibial facet (Fig. 99B). A substantial tibia-calcaneum contact was coded as present in *Elaphrosaurus*, *Ceratosaurus*, and Abelisauridae by Rauhut (2003). An isolated right calcaneum of *Masiakasaurus* (FMNH PR 2235) also bears a very large tibial facet (Carrano et al., 2002).

Tibia-calcaneum contact was coded as absent in *Coelophysis* (UCMP 129618), *Liliensternus* (MB R. 2175.14), *Dilophosaurus* (UCMP 37302), and *Syntarsus* (QG1. 184, 782) by Rauhut (2003). This is correct for *Liliensternus* (Fig. 99C) and probably also *Coelophysis* (Fig. 95C). The posterolateral ridge from the ascending process of the astragalus reaches the posterior rim of the astragalus medial to the calcaneum. The ridge

divides the tibial and fibular articular facets on the astragalus. The fibular facet extends to the posterior margin of the astragalar proximal surface, barring the tibia from contact with the calcaneum.

There is a small tibia-calcaneum contact and facet present in some specimens of *Dilophosaurus* (TMM 43646-61) (Fig. 100A-C), *Syntarsus rhodesiensis* (QG 786, and others), *"Syntarsus" kayentakatae* (MNA V2623, TMM 43669-3), and the Shake-N-Bake taxon (MCZ 9463) (Fig. 101). The character is seen best in disarticulated specimens, or at least those in which the fibula is removed. However, it is possible to make out a small tibia-calcaneum contact even in the heavily fused right tibiotarsus of MNA V2623 (Fig. 101C). The tibial contact on the calcaneum is a small oblique surface at the posteromedial corner of the calcaneum in these taxa. The facet is relatively flat and faces posteromedially and dorsally. The tibial facet is more concave in *Dilophosaurus* (TMM 43646-61).

The contact between the tibia and calcaneum was not previously recognized in specimens of *Dilophosaurus*. The left calcaneum of UCMP 37302 lacks a large, tetanuran-like tibial facet. The tibial facet of the astragalus clearly reaches the posterolateral corner of the bone, in contrast to the morphology in *Liliensternus*. It is likely that the tibia continued laterally a short distance to the calcaneum, as indicated by a small oblique surface on the calcaneum's posteromedial corner (Fig. 96A). The left calcaneum of UCMP 37303 bears a similar surface. Claims of no tibia-calcaneum contact in specimens of *Syntarsus rhodesiensis* are difficult to reconcile with descriptions

of the tarsus (Raath, 1977), and the feature is visible in photographs of several proximal tarsals (specimen numbers not given) assigned to the taxon (Raath, 1977).

252. Distal tarsal III remains separate (0), or fuses to (1) metatarsal III by adulthood (modified from Rowe, 1989; Rowe and Gauthier, 1990).

This character was deleted from the analysis of Rauhut (2003) because it was deemed too ontogenetically variable. This co-ossification was considered synapomorphic of Ceratosauria by Rowe (1989) and Rowe and Gauthier (1990), but given the limited number of mature specimens that preserve the pes it is difficult to support this assertion. The wording of the character here differs from that originally erected by Rowe (1989) and Rowe and Gauthier (1990). Their character descriptions included fusion of distal tarsal II to its metatarsal. An extensive review of the literature reveals that no ossified distal tarsal II is known from any adequately preserved and articulated fossil theropod. The type specimen of *"Syntarsus" kayentakatae* (MNA V2623) does not have a discernible distal tarsal II fused to its second metatarsal, contrary to previous statements (Rowe, 1989).

Fusion between distal tarsal III and metatarsal III is unambiguously present in some adult specimens of *Coelophysis*, *"Syntarsus" kayentakatae* (MNA V2623, TMM 43688-1), the Shake-N-Bake taxon (TMM 43689-4), and *Syntarsus rhodesiensis*. Distal tarsal III slightly overlaps the proximal end of metatarsal II in both the type and referred specimens of *"Syntarsus" kayentakatae*. The sub-adult "*Syntarsus*" *kayentakatae* individual TMM 43688-1 preserves the proximal ends of both tarsometatarsi (Fig. 102A-

C). Distal tarsal III is fused to the proximal end of metatarsal III on both sides, but open sutures are still visible around them. The third distal tarsal is almost indistinguishable from the third metatarsal in MNA V2623 (Fig. 102D, E).

The third distal tarsal contributes to the formation of a ventral enlargement of metatarsal III in these coelophysoid taxa. This opens the question as to whether ceratosauroid taxa that also bear a ventrally enlarged proximal third metatarsal (i.e. *Ceratosaurus*, *Elaphrosaurus*, *Aucasaurus*) might also possess fused third distal tarsals. Until this possibility can be explored and either confirmed or rejected the character is conservatively coded as absent in *Ceratosaurus*, *Elaphrosaurus*, and *Aucasaurus*. The character is coded as missing data in *Dilophosaurus* and *Liliensternus* because of the immature status of the specimens that preserve the metatarsals.

253. Distal tarsal IV round or sub-rectangular (0), or with large notch in posterlateral corner (1).

Distal tarsal IV is subtriangular in proximal and distal views in *Herrerasaurus* (identified only as the lateral distal tarsal by Novas, 1993), and basal sauropodomorphs (Cooper, 1981; Novas, 1993) (Fig. 103A). Its morphology is not entirely visible in the available cast of *Eoraptor*, but it also appears to be approximately equant in its dimensions. The fourth distal tarsal of many more derived theropods bears a large posterolateral notch that results in a "P" or reversed-"P" profile in proximal view (Fig. 103B, C). This morphology was appropriately described as "subpentagonal"by Coria et al. (2002). The posterior end of the tarsal has the appearance of a tuber or 'heel', and this

distal tarsal was probably the element identified as the calcaneum of *Segisaurus* by Camp (1936). This profile of the fourth distal tarsal is present in *Dilophosaurus*, *"Syntarsus" kayentakatae*, *Coelophysis*, *Syntarsus rhodesiensis*, the Shake-N-Bake taxon, *Ceratosaurus*, *Aucasaurus*, and *Allosaurus* among taxa in this analysis. The distribution of this character in other tetanurans is unclear because of the lack of material or descriptions. Distal tarsal IV is not noticeably notched in *Sinraptor dongi*, a taxon closely allied to *Allosaurus* (Currie and Zhao, 1993). The morphology is also absent in tyrannosaurs, but given the derived phylogenetic position of tyrannosaurs the absence of a posterolaterally notched distal tarsal four in these coelurosaurs has little informative value for basal theropod relationships.

254. Metatarsal I contacts ankle joint (0), or does not contact ankle joint (1) (modification of Gauthier, 1986; Rauhut, 2003).

255. Metatarsal I length ≥50% (0), or < 50% (1) length of metatarsal II (Gauthier, 1986).

256. Metatarsal I positioned on medial surface (0), or on ventral/plantar surface (1) of metatarsal II (Holtz, 1998).

The first metatarsal lies in the approximately the same plane as the other four metatarsals in *Marasuchus*, ornithischians, *Herrerasaurus*, basal sauropodomorphs, and *Eoraptor* (Novas, 1993; Sereno and Arcucci, 1994). The first digit was repositioned to the ventral/plantar surface of the pes in many tetanuran taxa, and this condition was

correctly coded as present in tetanurans in previous analyses (Holtz, 1998). The coelophysoid pes was consistently reconstructed or restored with the first digit aligned in the same plane with metatarsals II through V (Raath, 1969, 1977; Welles, 1984; Colbert, 1989), and the character was coded as absent in coelophysoid taxa by Holtz (1998). Articulated specimens of *Dilophosaurus* (TMM 43646-61) (Fig. 104A), *"Syntarsus" kayentakatae* (MNA V2623) (Fig. 104B), and the Shake-N-Bake taxon preserve metatarsal I tightly appressed to the ventral (or posterior) side of metatarsal II. The distal end of metatarsal I is directed distolaterally so that the contact between the metatarsal and the first phalanx is ventral to metatarsal III in these specimens. The shaft of metatarsal I is also positioned ventral to the rest of the metatarsals in *Segisaurus*, although the distal end of the metatarsal is directed distomedially rather than distolaterally as in the specimens cited above (Fig. 104C). I code this character as present in these coelophysoid taxa.

257. Proximal ends of metatarsals II and III remain separate (0), or co-ossify to each other (1) by adulthood (Rowe, 1989).

Co-ossification between the proximal ends of metatarsals II and III in a coelophysoid was first noted and described by Raath (1969, 1977) in *Syntarsus rhodesiensis*. Fused metatarsals II and III were later described in the type specimen of *"Syntarsus" kayentakatae*. This provided support at the time for a very close relationship between the African and North American taxa, to the exclusion of other coelophysoids.

Similar metatarsal fusion is now known in some specimens of *Coelophysis* (MNA V3328, CMNH 11892, CMNH 11893), and in the Shake-N-Bake taxon (TMM 43689-4).

Only large individuals of *Syntarsus rhodesiensis* exhibit metatarsal fusion (Raath, 1977), but the distribution of this feature may not be strictly related to size (and age) in *Coelophysis* (Colbert, 1990). The holotype of *"Syntarsus" kayentakatae* (MNA V2623) is an adult individual, and the proximal ends of metatarsals II and III are extensively fused. A sub-adult of the taxon (TMM 43688-1) exhibits an intermediate stage of metatarsal fusion. The proximal ends of both the left and right metatarsals II and III were recovered. The proximal ends of the right-side metatarsals are co-ossified. The left-side metatarsals are not co-ossified. The results of the ontogenetic study (see Chapter 1) suggest that metatarsal fusion occurred during mid- to late sub-adulthood in robust *"Syntarsus" kayentakatae* individuals after fusion of the third distal tarsal to metatarsal III.

The known specimens of *Liliensternus* and most of the specimens of *Dilophosaurus* arenot individuals mature enough to evaluate this character, assuming the ontogenetic trajectory and relative timing of co-ossifications are consistent among coelophysoids. The only adult *Dilophosaurus* specimen (UCMP 77270) does not preserve the pes, so it offers no insight as to the presence of the character in the taxon. This character is coded as missing data for these two taxa. The shafts of metatarsals II and III of *Segisaurus* are very tightly pressed against one another, whereas metatarsal IV is not so tightly bound to III (Fig. 104C). The same relationship is present in the type and referred specimens of *"Syntarsus" kayentakatae*. This could be a sign that metatarsals II

and III were also co-ossified in *Segisaurus*. This cannot be confirmed though because the proximal ends of metatarsals II and III are not preserved with the type and only known specimen of *Segisaurus*. It is clear that fusion between metatarsals II and III is more widely distributed among coelophysoids than first thought. Only future finds will determine if the character is diagnostic of Coelophysoidea as a whole.

258. Mediolateral width of metatarsal II shaft approximately = widths of III and IV (0), or < width of IV and both < III (1) (Carrano et al., 2002).

259. Proximal end of metatarsal III does not back ventral side of metatarsals II and IV (0), or backs metatarsals II and IV ventrally, resulting in "T"-shaped proximal profile ("antarctometatarsus") (1).

The proximal end of metatarsal III is not expanded or enlarged relative to the adjacent metatarsals in theropod outgroups, nor in tetanurans (Fig. 105A). In *Allosaurus* and other basal tetanurans, the proximal end of metatarsal III is broadest near its dorsal (anterior) side (Fig. 105B). It was later recognized that some coelophysoids and neoceratosaurs have a derived condition of metatarsal III in which the ventral (posterior) side of the proximal end is broader relative to its dorsal (anterior) side (Novas, 1989a). This was labeled an "antarctometatarsus" condition in a later character description (Carrano et al., 2002). The character was coded as present only in *Elaphrosaurus*, *Ceratosaurus*, and the abelisaurid *Majungatholus* at that time. The proximal profile of metatarsal III's proximal end is shaped like an inverted "T" in *Elaphrosaurus* and

Ceratosaurus (Fig. 105C, D). The medial and lateral branches of the "T" underlay the ventral surfaces of proximal ends of metatarsals II and IV. A ventral enlargement was also reported on the proximal metatarsal III of *Aucasaurus*, and its description suggests it also backs at least the proximal end of metatarsal IV (Coria et al., 2002).

The proximal end of metatarsal III is also ventrally enlarged in several coelophysoids, as previously recognized (Novas, 1989a). Its proximal end is weakly "T"-shaped in *Coelophysis* and *"Syntarsus" kayentakatae* (Fig. 105E), but much more strongly so in *Syntarsus rhodesiensis* (Fig. 105F). In all three of these taxa the proximal end of metatarsal III ventrally backs metatarsals II and IV. In addition to the mediolateral expansion shared with the ceratosauroids cited above, several coelophysoid taxa have a further ventral (posterior) enlargement of metatarsal III. The proximal end of the third metatarsal is enlarged ventrally to form a prominent, rounded tuber or boss in *Liliensternus* (Huene, 1934:pl. 15, fig. 18b) *Coelophysis*, *"Syntarsus" kayentakatae* (Fig. 105E), and *Syntarsus rhodesiensis* (Fig. 105F). The boss protrudes ventrally well beyond the plane of the rest of the metatarsals and the rest of the shaft of metatarsal III (Fig. 105G). The ventral side of the proximal end of metatarsal III is flat in *Elaphrosaurus* and *Ceratosaurus*. The prominent boss is listed as a separate character below (character 304). There is no evidence for a ventral tuberosity or expansion on metatarsal III of any *Dilophosaurus* specimen in which the element is preserved.

The relative size and mediolateral breadth of the metatarsal III ventral expansion in the sub-adult *"Syntarsus" kayentakatae* specimen TMM 43688-1 is less than in the adult holotype specimen (MNA V2623) (Figs. 102, 105G, H). There is not yet enough

information to categorize this character as strictly a result of ontogeny. It should be kept in mind for future consideration if and when additional specimens of more mature *Dilophosaurus* and *Liliensternus* individuals are recovered.

260. Proximal end of metatarsal III not ventrally enlarged (0), or with ventral boss protruding beyond plane of metatarsal shafts (1).

261. Metatarsal V with distal articular surface (0), or lacks distal articulation (1) (Gauthier, 1986; Rauhut, 2000).

262. Metatarsal V shaft round and straight (0), or mediolaterally flattened and distal end angles dorsally (anteriorly) (1) (modified from Gauthier, 1986; Rauhut, 2003).

263. Pedal unguals with single lateral groove (0), or two lateral grooves (1) (Sampson et al., 2001; Novas and Bandyopadhyay, 2001).

264. Ungual of pedal digit II symmetrical (0), or asymmetrical (1) (Carrano et al., 2002).

CHAPTER 3

Phylogenetic Analysis: Results and Discussion

Three separate phylogenetic tests were run. The first two phylogenetic tests were conducted to approximate the methods most often used by previous workers to address the ontogenetic variability preserved in pertinent coelophysoid fossils. The first test scored ontogenetically dependent characters as if all the taxa were represented by adult specimens that expressed the mature morphological condition of all the characters. The second test identified and deleted maturity-dependent characters from the analysis, following the approach of Rauhut (2003). The third test incorporated the results of the ontogenetic analysis (see Chapter 1), in which taxa were coded to reflect whether they were represented by specimens ontogenetically developed enough to express maturity-dependent characters prior to the animal's death. The remaining characters in the data matrices used in the first three tests were the same, and included new data derived from new specimens as well as reinterpretation of some characters and morphologies from previous works. This isolated the different approaches to ontogeny estimation as the only variable between the three tests.

The purpose of the first two tests was to determine the effects of ontogenetic considerations in scoring on tree topology. These tests did not utilize my preferred method of dealing with the ontogenetic status of the known specimens, and the character diagnoses from the first two tests are not given. A complete list of the character

diagnoses for pertinent saurischian nodes in the third test is provided. I acknowledge that only nodes are diagnosed under cladistic phylogenetic reconstruction. Stem clades such as Theropoda, Coelophysoidea, Ceratosauria, Ceratosauroidea, and Tetanurae do not technically bear diagnoses. Diagnoses are provided for the most basal node recovered within each of these stem clades. The taxonomic content of the most basal node on a stem-lineage is indicated following the stem-defined clade name. See Table 1 for the definitions of the clade names used in this chapter.

Phylogenetic Test 1: all taxa scored as adults.

This test followed an assumption implicit but probably unintentional in many previous phylogenetic analyses of basal theropod relationships, which was that all taxa were treated as if they were known from mature individuals. The major difference between this test set and my preferred test set (Test 3) was the scoring of *Dilophosaurus*, *Liliensternus*, and *Segisaurus*. These taxa were also coded as if they were represented by adult specimens in the character-taxon matrix of this test. The analysis was run with 264 total characters scored for 28 ingroup and four outgroup taxa. The analysis resulted in 70 equally most parsimonious trees, with a length of 619, consistency index of 0.4895, and retention index of of 0.7288. Ceratosauria was the monophyletic sister taxon to Tetanurae in all trees, with Coelophysoidea the sister taxon to Ceratosauroidea, (Fig. 106A-C). The recovered tree topologies were inconsistent with the phylogenetic hypotheses of Carrano et al. (2002), Rauhut (2003), and Wilson et al. (2003) in this regard, but consistent with the results of Holtz (1998). *Liliensternus*, considered the

sister taxon to Coelophysidae in most other analyses, was placed as the most basal ceratosaurian, an unexpected result. Ceratosauroidea consisted of *Elaphrosaurus*, *Ceratosaurus*, and Abelisauria as successively more derived taxa. The monophyly of Tetanurae was strongly supported, with an *Eustreptospondylus* + *Allosaurus* + *Ornitholestes* clade the sister taxon to a *Torvosaurus* + "*Poekilopleuron*" *valedunensis* and *Irritator* + *Baryonyx* + *Suchomimus* clade.

Relationships within Coelophysoidea were incompletely in the strict consensus tree (Figure 106A). *Dilophosaurus* was the most basal coelophysoid in the analysis in all cases, a position contrary to previous results that placed *Dilophosaurus* closer to Tetanurae than to *Coelophysis* (Carrano et al., 2002; Rauhut, 2003). *Zupaysaurus* was in a more derived position than *Dilophosaurus*, followed by a polytomy consisting of the Shake-N-Bake taxon, *Coelophysis*, *Syntarsus rhodesiensis*, *Segisaurus*, and "*Syntarsus*" *kayentakatae* (Fig. 106A). In most of the recovered trees, *Coelophysis* and *Syntarsus rhodesiensis* formed a clade, and *Segisaurus* and "*Syntarsus*" *kayentakatae* formed another (Fig. 106B, C).

The sister taxon relationship between Coelophysoidea and Ceratosauroidea was not expected, given the coding technique applied to maturity dependent characters in *Dilophosaurus*, *Liliensternus*, and *Segisaurus*. It was expected that Coelophysoidea would be excluded from Ceratosauria, as had been recovered by Carrano et al. (2002). I believe new data and differences in interpretation of a number of characters in *Dilophosaurus*, *Coelophysis*, *Syntarsus rhodesiensis*, and "*Syntarsus*" *kayentakatae* resulted in substantially different character polarity and reconstructions of character

evolution at the base of Theropoda and Coelophysoidea than was available to previous workers. The postcranial elements of *Dilophosaurus* specimens UCMP 77270 and TMM 43646 were especially important to these reinterpretations. The remains of these two individuals revealed several unequivocal features shared by *Dilophosaurus* and other coelophysoids, which firmly nested the taxon on the coelophysoid lineage independently of how maturity-dependent characters were treated in the analysis.

The basal position of *Liliensternus* relative to the rest of Ceratosauria can be attributed to the approach taken in coding maturity-dependent characters in this test, combined with the incompleteness of the specimen with regard to parts of the skeleton that possess diagnostic apomorphies of more derived ceratosaurian clades. No adult specimens of *Liliensternus* are known, as indicated by the results of the ontogenetic analysis (Chapter 1). In contrast, almost all the other coelophysoid taxa in the analysis were represented by at least one adult specimen that exhibited the derived states of at least some maturity-dependent characters. The basal position of *Liliensternus* in the results of Test 1 leads to the following conclusion. An immature taxon (=a taxon represented only by fossils of immature individuals) will fall to a relatively basal position in the results of a cladistic analysis dominated by mature taxa (=taxa represented by fossils of mature individuals that preserve derived states of maturity-dependent characters), and in which maturity-dependent characters are coded without regard for immature taxa. In other words, an 'all-adults' approach to coding maturity-dependent characters has the potential to place immature taxa in artificially basal positions in hypotheses generated by a cladistic analysis.

Phylogenetic Test 2: maturity-dependent characters deleted.

The same taxon-character matrix used in phylogenetic test 3 was also used in this test set, except that maturity-dependent characters were deleted from the analysis. This approximated the approach taken by some workers (Rauhut, 2003) when confronted by highly variable, or poorly understood, maturity-dependent characters. In all, 27 characters were removed from consideration in this test set. The deleted characters are listed in Table 6. The analysis was run using the remaining 237 parsimony-informative characters. The same 28 ingroup and four outgroup taxa were used as in phylogenetic test 1. The analysis resulted in the recovery of 1008 equally most parsimonious trees with a length of 544 evolutionary transformations, a consistency index of 0.5000, and a retention index of 0.7323.

The resulting trees were different from those generated in the previous test (Fig. 107A-C). Coelophysoidea was unequivocally the proximal sister taxon to Neotheropoda, and not a member of Ceratosauria. The results were consistent with the findings of Carrano et al. (2002), Rauhut (2003), Wilson et al. (2003), and Sereno et al. (2004). Ceratosauria was monophyletic in all trees, but relationships within Ceratosauria were unresolved (Fig. 107A). *Ceratosaurus* was the basal most ceratosaur in most of the recovered trees, with *Elaphrosaurus* usually the next most derived ceratosaurian taxon (Fig. 107B, C). Noasauridae and a *Majungatholus* + *Aucasaurus* + *Carnotaurus* clade were the only ceratosaur clades consistently recovered. Tetanurae was also supported in all the trees.

Coelophysoid relationships were generally similar to those recovered in phylogenetic test 1 (Fig. 107A). The major difference was that *Liliensternus* was found to be a coelophysoid theropod, a result consistent with previous analyses (Holtz, 1998; Carrano et al., 2002; Rauhut, 2003). *Dilophosaurus* occupied the basal position in Coelophysoidea, contrary to the hypotheses of Carrano et al. (2002), and Rauhut (2003), which each found *Dilophosaurus* was closer to the neotheropod clade than to the coelophysoids. *Zupaysaurus* and *Liliensternus* competed for the next most derived coelophysoid position. The Shake-N-Bake taxon was a labile taxon among the coelophysids, and was part of a polytomy that also included a *Coelophysis* + *Syntarsus rhodesiensis* clade and a *Segisaurus* + "*Syntarsus*" *kayentakatae* clade on the Adams consensus tree (Fig. 107B).

Phylogenetic Test 3: Incorporation of ontogenetic analysis results.

This test used an unaltered version of the character-taxon matrix. Characters likely to be expressed only in later stages of ontogeny were treated as missing data in coelophysoid taxa represented by insufficiently mature specimens, which was determined in the ontogenetic analysis in Chapter 1. The results of this analysis are given in greater detail than for phylogenetic tests 1 and 2 (Fig. 108A-F). Character diagnoses are given below for all coelophysoid and ceratosauroid clades recovered in the hypothesis of phylogeny illustrated in Figure 108D, as well as the more basal saurischian clades and the most basal node within Tetanurae. Diagnoses for the most basal nodes within stem-defined lineages are given, with explicit indication of reference taxa used in my analysis

that encompass such nodes. Reference taxa used in the analysis are also provided for node-defined clades for the sake of clarity. Nodes that do not bear a formal phylogenetically defined name are indicated by two reference taxa that encompass the taxonomic content of the node. The reference taxa used in the diagnoses below are not necessarily the same as those used to define the clade names, because some taxa used to phylogenetically define the names were not OTUs in this analysis (e.g. Aves).

Phylogenetic test 3 used 28 ingroup taxa, and four outgroup taxa, which were scored for 264 parsimony-informative characters. The analysis of the data resulted in 1050 equally most parsimonious trees, with a length of 608, a consistency index of 0.4984, and a retention index of 0.7362. *Herrerasaurus* was the most basal theropod in the analysis, with *Eoraptor* the sister taxon to Neotheropoda. Coelophysoidea was included within Ceratosauria in all the trees (Fig. 108A), supporting the taxonomic content of Ceratosauria in the sense of Gauthier (1986), Rowe (1989), Rowe and Gauthier (1990), Holtz (1994, 1998), Rowe et al. (1997), Sereno (1998, 1999a), and Tykoski and Rowe (2004). *Dilophosaurus* occupied the most basal position among the coelophysoids, and *Liliensternus* and *Zupaysaurus* vied for the next more derived coelophysoid position (Fig. 108A-D). It required four additional evolutionary steps to remove Coelophysoidea to a position outside a Ceratosauroidea + Tetanurae clade. It took 24 additional steps to place Coelophysoidea basal to a Ceratosauroidea + Tetanurae clade, remove *Dilophosaurus* from Coelophysoidea, and place *Dilophosaurus* as the proximal outgroup to the Ceratosauroidea + Tetanurae clade (as per Carrano et al., 2002; Rauhut, 2003).

There was support for a clade comprised of *Coelophysis*, *Syntarsus rhodesiensis*, *"Syntarsus" kayentakatae*, *Segisaurus*, and the Shake-N-Bake taxon. Resolution within this clade was poor in the strict consensus tree because of the lability of the Shake-N-Bake taxon within it. Adams consensus and 50% majority rule consensus trees showed the Shake-N-Bake taxon in a basal polytomy with a *Coelophysis* + *Syntarsus rhodesiensis* clade and a *Segisaurus* + *"Syntarsus" kayentakatae* clade (Fig. 108B, C). *Syntarsus rhodesiensis* and *"Syntarsus" kayentakatae* did not comprise a monophyletic group in any of the recovered trees. It required at least six additional evolutionary steps to make *Syntarsus rhodesiensis* and *"Syntarsus" kayentakatae* sister taxa and retain *Coelophysis* as the proximal outgroup to the *Syntarsus rhodesiensis* + "*Syntarsus*" *kayentakatae* clade. It took five additional steps to make *Syntarsus rhodesiensis* and "*Syntarsus*" *kayentakatae* sister taxa, place *Segisaurus* as the sister taxon to that clade, and position *Coelophysis* as the proximal outgroup to that clade. It is uncertain at which node the name Coelophysidae should be applied. The name Coelophysidae was phylogenetically defined as the clade comprised of *Coelophysis* + *Syntarsus*, and all descendants of their most recent common ancestor (Holtz, 1994; Table 1). *"Syntarsus" kayentakatae* has traditionally been viewed as a coelophysid theropod, (as has *Segisaurus*), and the name Coelophysidae was phylogenetically defined under the assumption that *Syntarsus rhodesiensis* and "*Syntarsus*" *kayentakatae* were sister taxa (Holtz, 1994; Tykoski, 1998; Sereno, 1999a; Carrano et al., 2002). Either the name Coelophysidae must be redefined to encompass *"Syntarsus" kayentakatae* when its name

is formally revised, or the term Coelophysidae must be restricted to the clade comprising only *Syntarsus rhodesiensis* and *Coelophysis bauri* (Fig. 108E).

I advocate altering the definition of the name Coelophysidae so that it also encompasses "*Syntarsus*" *kayentakatae* and *Segisaurus halli*. These taxa consistently group with *Coelophysis bauri* and *Syntarsus rhodesiensis*, and often the Shake-N-Bake taxon, to form a clade of small-bodied coelophysoids distinguishable from other coelophysoids such as *Dilophosaurus* and *Liliensternus*. There is also a history of use of the name (Holtz, 1994; Tykoski, 1998; Sereno, 1999a; Carrano et al., 2002) that includes these taxa. Removal of "*Syntarsus*" *kayentakatae* and *Segisaurus* from the clade as defined could generate confusion. Given the incompleteness of the type and only specimen of *Segisaurus halli*, I urge "*Syntarsus*" *kayentakatae* eventually be used as a reference taxon for defining Coelophysidae in conjunction with *Coelophysis bauri*.

Ceratosauroidea was the sister taxon of Coelophysoidea given the relationships recovered in my analysis. *Elaphrosaurus* and *Ceratosaurus* vied for status as the most basal member of the ceratosauroid lineage. It required only two additional steps to make *Elaphrosaurus* a basal coelophysoid, whereas it required 13 additional steps to ally *Ceratosaurus* with the coelophysoids. *Noasaurus* and *Masiakasaurus* formed a well-supported clade more derived than *Elaphrosaurus* and *Ceratosaurus*, near the base of the abelisauroid lineage. *Xenotarsosaurus* and *Ilokelesia* were both variable in their position relative to *Abelisaurus* and the other abelisaurids in the analysis, so it is uncertain at this time if the latter two taxa should be considered abelisaurids or non-abelisaurid

abelisauroids. There was a well-supported clade within Abelisauridae consisting of *Majungatholus*, *Aucasaurus*, and *Carnotaurus*.

A heuristic bootstrap analysis of the data (1000 replicates) yielded greater than 50% support for a majority of the recovered clades (Fig. 108F). There was very high bootstrap support for Neotheropoda (99.5%). The two major neotheropod lineages were each supported as well (Ceratosauria 62.3%, Tetanurae 78.6%). Coelophysoidea was supported in 70.2%, and Ceratosauroidea in 64.7% of the bootstrap replicates. There was also substantial support for Noasauridae (88.5%), and Abelisauria (85.6%). Among the coelophysoids there was support for a clade of taxa more derived than *Dilophosaurus* (59.1%), a coelophysid clade that included the Shake-N-Bake taxon (66.1%), and a *Segisaurus* + "*Syntarsus*" *kayentakatae* clade (55.1%). There was little bootstrap support (14.0%) for a Ceratosauria + Tetanurae clade that excluded Coelophysoidea from the Ceratosauria.

Decay analysis of the data revealed weak to moderate support for most of the clades recovered in the analysis (Fig. 108A). Low decay indices were recovered for the *Ilokelesia* + *Carnotaurus* clade (1), the *Majungatholus* + *Carnotaurus* clade (1), the *Aucasaurus* + *Carnotaurus* clade (1), the *Irritator* + *Suchomimus* clade (1), the *Baryonyx* + *Suchomimus* clade (1), *Herrerasaurus* + Neotheropoda clade (1), the *Allosaurus* + *Ornitholestes* clade (2), the *Liliensternus* + *Coelophysis* clade (2), the Shake-N-Bake taxon + *Coelophysis* clade (2), and Abelisauria (2). Moderate decay indices were indicated for the *Plateosaurus* + Neotheropoda clade (3), the basal node of Tetanurae (3), the *Eoraptor* + Neotheropoda clade (4), the basal node of Ceratosauria (4),

Noasauridae (4), and the basal node of Coelophysoidea (5). High decay indices were recovered for the *Lesothosaurus* + *Scutellosaurus* clade (7), the basal node within Ceratosauroidea (11), and Neotheropoda (18).

Diagnoses for clades in Figure 108D

Diagnoses for each saurischian node in Figure 108D are given below. Each set of character diagnoses is divided into unambiguous and ambiguous characters. Ambiguous characters at each node are each preceded by either "(A)" or "(D)" to denote whether they are diagnostic under ACCTRAN or DELTRAN character state optimization respectively. Transformations are from state "0" (primitive) to state "1" (derived) unless otherwise indicated because of reversals, or transformation to other derived states in multistate characters. Transformation direction in such a case is indicated by parentheses following the chracter number that contains the states and transformation direction. For exmaple, "(1→0)" means from state "1" to state "0", and "(0→2)" means from state "0" to state "2".

Saurischia (node diagnosed = *Plateosaurus* + all other saurischians)

Unambiguous apomorphies:

109. Transverse processes of postaxial presacral vertebrae ventrally braced by centrodiapophyseal laminae.

110. Cervical epipophyses are low ridges.

246. Tibial facet of astragalus deep and extends posterior to base of ascending process.

Ambiguous apomorphies:

(A) 11. Maxillary process of premaxilla dorsoventrally narrow and rod-like.

(A) 19. Anterodorsal margin of maxilla is anterodorsally concave.

(A) 44. Nasal contributes to border of antorbital cavity.

(A) 53. Lacrimal dorsoventrally as tall or subequal to height of orbit with ventral end that reach level of orbit's ventral rim.

(A) 91. Splenial with foramen (either closed or ventrally open) near anteroventral margin

(A) 123. Neural spines of post-axial cervicals dorsoventrally low.

(A) 138. Hyposphene-hypantrum articulations present on dorsal vertebrae.

(A) 172. Humerus shaft torsion present.

(A) 181. Proximal half or more of metacarpal I closely appressed to metacarpal II.

(A) 217. Distal tip of ischium anteroposteriorly enlarged ≤3 times minimum anteroposterior width of ischial shaft.

(D) 119(1→0). Axial neural spine stops posterior to prezygapophyses.

(D) 138. Hyposphene-hypantrum articulations present on dorsal vertebrae.

Theropoda (node diagnosed = ***Herrerasaurus*** **+** ***Allosaurus*** **clade**

Unambiguous apomorphies:

70. Posterior process of jugal divided, ventral prong subequal or much shorter than dorsal prong.

72. Ventral process of squamosal broad and/or expanded.

158. Neural arch elements (transverse processes, neural spines) reduced in distal caudal vertebrae

159(0→2). Distal caudal vertebral zygapophyses with ≥50% overlap of preceding centrum.

178. Distal ends of metacarpals with deep, well-developed extensor pits.

184. Manual digit II penultimate phalanx (II-2) length > length of phalanx II-1.

186. Metacarpal IV much smaller than metacarpal III.

187. Manual digit IV ≤1 phalanx.

188. Manual digit V is at most a vestigial metacarpal that lacks phalanges.

239. Fibular M. iliofibularis insertion a distinct small tubercle.

Ambiguous apomorphies:

(A) 24. Ratio of dorsoventral height of proximal end of anterior process of maxilla versus height of alveolar ramus of maxilla at first alveolus posterior to rim of internal antorbital fenestra ≥1.0.

(A) 38. Anteromedial/palatal process of maxilla medial surface bears longitudinal ridges.

(A) 71. Lateral surface of jugal with low rounded ridge that traverses anterior and posterior processes.

(A) 143. Neural spines of posterior dorsal vertebrae substantially taller than anteroposteriorly long.

(A) 153. Sacral ribs and transverse processes fuse to ilia in adults.

(A) 182. Phalanx I-1 length/metacarpal I length >1.0.

(A) 210(0→2). Distal tip of pubis ≥3 times anteroposterior width of pubic shaft.

***Eoraptor* + *Allosaurus* clade**

Unambiguous apomorphies:

52. Lacrimal an inverted L-shape in lateral view.

146. Vertebra 25 incorporated into sacral series (as dorsosacral 1).

193. Preacetabular process of ilium relatively thin and blade-like.

197. Ilium postacetabular length > acetabulum width.

205. Proximal pubic plate ventromedial to obturator foramen with pubic fenestra.

236. Tibia distal profile subrectangular with small posterolateral extension.

Ambiguous apomorphies:

(A) 8(1→0). Premaxilla nasal process comprises >50% external naris anterodorsal border.

(A) 59. Lacrimal antorbital fossa or large, excavates laterally open triangular fossa on lacrimal ventral ramus.

(A) 78. Basisphenoid lateral surface excavated by anterior tympanic recess.

(A) 82. Ventral edge of proximal end of paroccipital process at same level or ventral to horizontal plane through middle of occipital condyle.

(A) 84. Ectopterygoid flange of pterygoid marked by fossa.

(A) 94. Retroarticular process of mandible or much broader than mandible anterior to jaw joint.

(A) 104. Anterior articular surfaces of anterior cervical centra wider than tall.

(A) 114. Axis bears pleurocoels.

(A) 207. Pubic shaft axis curves ventrally, resulting in anterior bowing (convex anterior, concave posterior) of shaft in lateral view.

(A) 216. Obturator process of ischium distally separated from ischial shaft by notch.

(A) 220. Femoral head set off by well defined oblique ligament groove on posterior surface, giving 'hooked' proximal profile to femoral head.

(A) 222(0→2). Femoral anterior trochanter a mediolaterally compressed flange (=aliform process) projecting anteriorly from femur.

(A) 224. Femoral trochanteric shelf expressed as low mound or swelling distolateral to anterior trochanter in adults.

(A) 225. Medial epicondyle of femur strongly developed ridge.

(A) 230. Lateral surface of cnemial crest of tibia excavated by longitudinal fossa, giving tibia laterally 'hooked' profile in proximal view.

(A) 231. Proximal condyles of tibia separated by cleft along posterior rim of tibia in proximal view.

(A) 233. Fibular crest (=crista fibularis) of tibia a low ridge extending distally from proximal tibia.

(A) 243. Fibular facet on proximal surface of astragalus large, does not reach posterior rim of astragalus.

(A) 244. Ascending process of astragalus height ≥ height of main body of astragalus.

(A) 247. Ascending process of astragalus or anteroposteriorly flattened.

(A) 248. Anterior surface of astragalus traversed by horizontal groove.

(A) 251. Calcaneum with small tibial facet on posteromedial corner.

(A) 261. Metatarsal V lacks distal articulation.

(D) 11. Maxillary process of premaxilla narrow and rod-like.

(D) 19. Anterodorsal margin of maxilla anterodorsally concave in lateral view.

(D) 44. Nasal excluded contributes to border of antorbital cavity.

(D) 53. Lacrimal dorsoventrally as tall or subequal to height of orbit with ventral end that reach level of orbit's ventral rim.

(D) 59. Lacrimal antorbital fossa large, excavates laterally open triangular fossa on lacrimal ventral ramus.

(D) 172. Humerus shaft torsion present.

(D) 181. Metacarpal I with strongly asymmetrical distal articular condyles, medial condyle more proximal than lateral condyle.

(D) 217. Distal tip of ischium anteroposteriorly enlarged ≤3 times minimum anteroposterior width of ischial shaft.

Neotheropoda (=*Ceratosaurus* + *Allosaurus*)

Unambiguous apomorphies:

3. Orbit keyhole-shaped with narrower ventral end.

4. Orbit anteroposterior diameter < internal antorbital fenestra length.

18. Subnarial foramen along premaxilla-maxilla contact.

23. Anterior process of maxilla length 10% < 25% total maxilla length.

43. Lateral surface of anterior end of nasal along margin of external naris with concave fossa.

70(1→2). Posterior process of jugal divided with ventral prong much longer than dorsal prong.

79. Basisphenoidal recess deep and well developed.

103. Posterior articular surfaces of cervical and anterior dorsal centra deeply concave.

105. Anterior pleurocoels in post-axial cervical centra.

145. Vertebra 24 incorporated into sacral series (as dorsosacral 2).

185. Manual digit III penultimate phalanx (III-3) length > length of each of the more proximal digit III phalanges.

188(1→2). Manual digit V is absent.

192. Preacetabular process of ilium extends anteriorly well past pubic peduncle.

206. Mediolateral width of pubic <25% overall shaft length.

212. Distal tip of pubis subtriangular in distal view.

226. Anterior surface of femoral distal end with broad, shallow, depression bordered medially by medial epicondyle in adults.

234. Tibia and fibula closely appressed through most of shafts' length.

235. Distal end of tibia with broad anterior fossa bearing oblique (proximolateral to distomedial) proximal border.

237. Medial side of proximal end of fibula excavated by longitudinal groove.

240. Anteroposterior midshaft width of fibula ≤ 30% anteroposterior width of proximal end of fibula.

245. Ascending process of astragalus positioned near anteroproximal margin of astragalus.

253. Distal tarsal IV with large notch in posterlateral corner.

254. Metatarsal I does not contact ankle joint.

255. Metatarsal I length < 50% length of metatarsal II.

256. Metatarsal I positioned on ventral/plantar surface of metatarsal II.

Ambiguous apomorphies:

(A) 12. Maxillary process of premaxilla does not contact nasal, allowing maxilla to contribute to rim of external naris

(A) 34. Promaxillary fenestra of maxilla present, clearly visible in lateral view.

(A) 66. Anterior process of postorbital at about same level as posterior process, resulting in T-shaped postorbital.

(A) 71. Lateral surface of jugal with low rounded ridge that traverses anterior and posterior processes.

(A) 96. Mesial premaxillary teeth cross-section subcircular.

(A) 107. Cervical pleurocoels present as deep ovoid fossae or pockets.

(A) 110(1→3). Cervical epipophyses strongly developed, and project mostly dorsally above zygapophyses.

(A) 133. Cervical rib heads marked by pneumatic excavations.

(A) 136. Anterior dorsal vertebrae with pleurocoel in anterior half of centrum.

(A) 161. Anterior processes on proximal end of haemal arches (chevrons) are small tubercules.

(A) 162. Furcula (=median fusion of clavicles) present.

(A) 164. Distal end of scapular blade not expanded.

(A) 168. Posteroventral process of coracoid expanded beyond margin of glenoid fossa.

(A) 177. Distal carpals I and II fuse to each other, resulting in single element proximally capping metacarpals I and II.

(A) 183. Manual digit II is longest of the manus.

(A) 194. Ventral rim of preacetabular process of ilium with ventral expansion or 'hook'.

(A) 200. Pubic peduncle of ilium size much greater than ischial peduncle.

(A) 208. Medial lamina of pubis stops short of distal tip of pubic shaft, resulting in short median separation between distal tips of pubes.

(A) 236. Tibia distal profile subtriangular with large posterolateral expansion.

(D) 24. Ratio of dorsoventral height of proximal end of anterior process of maxilla versus height of alveolar ramus of maxilla at first alveolus posterior to rim of internal antorbital fenestra ≥1.0.

(D) 38. Medial surface of anteromedial process of maxilla bears longitudinal ridges.

(D) 78. Basisphenoid lateral surface excavated by anterior tympanic recess.

(D) 91. Splenial with foramen (either closed or ventrally open) near anteroventral margin.

(D) 104. Anterior articular surfaces of anterior cervical centra wider than tall.

(D) 210. Distal tip of pubis enlarged 2<3 times anteroposterior width of pubic shaft.

(D) 220. Femoral head set off by well defined oblique ligament groove on posterior surface, giving 'hooked' proximal profile to femoral head.

(D) 222. Femoral anterior trochanter a mediolaterally compressed flange (=aliform process) projecting anteriorly from femur.

(D) 224. Femoral trochanteric shelf expressed as low mound or swelling distolateral to anterior trochanter.

(D) 225. Medial epicondyle of femur a strongly developed ridge.

(D) 230. Lateral surface of cnemial crest of tibia excavated by longitudinal fossa, giving tibia laterally 'hooked' profile in proximal view.

(D) 231. Proximal condyles of tibia separated by cleft along posterior rim of tibia in proximal view.

(D) 243. Fibular facet on proximal surface of astragalus large, does not reach posterior rim of astragalus.

(D) 248. Anterior surface of astragalus traversed by horizontal groove.

(D) 251. Calcaneum with small tibial facet on posteromedial corner.

Tetanurae (node diagnosed = *Allosaurus* + *Torvosaurus*)

Unambiguous apomorphies:

29. Maxillary tooth row ends anterior to anterior rim of orbit.

57. Lacrimal antorbital fossa with deep pneumatic recesses in posterodorsal corner of lacrimal.

60. Lacrimal with distinct "horn" (=posterodorsal boss or blade).

69. Jugal does not contact internal antorbital fenestra, participates in external antorbital fenestra.

81. Cranial nerves X and XI exit skull through foramen/foramina on posterior skull surface lateral to occipital condyle and foramen for cranial nerve XII.

102. Anterior articular surfaces of cervical and anterior dorsal centra strongly convex, ball-like.

108. Internal pneumatic cavities in vertebral centra are camerate.

117. Axial neural spine and epipophyses/postzygapophyses connected by continuous laminae

180. Proximal half or more of metacarpal I closely appressed to metacarpal II

186(1→2). Metacarpal IV absent.

218. Femoral head oriented strictly medially when distal condyles set perpendicular to axial column.

219. Femoral head directed horizontally or slightly dorsally.

223. Femoral anterior trochanter reaches proximally at least to mid-point of femoral head.

243(1→2). Fibular facet on proximal surface of astragalus is a small subtriangular fossa on anterolateral corner of proximal surface of astragalus.

251(1→2). Calcaneum with large tibial facet covering most of posterior surface and reaches nearly to lateral edge of calcaneum.

<u>Ambiguous apomorphies</u>:

(A) 8. Premaxilla nasal process comprises > 50% (0), or ≤ 50% (1) of external naris anterodorsal border.

(A) 34(1→2). Promaxillary fenestra of maxilla present and concealed from lateral view by lateral lamina of maxillary antorbital fossa.

(A) 73. Quadratojugal and squamosal contact broad.

(A) 85(0→2). Ectopterygoid ventral surface with fossa and deep groove excavated into body of element from medial side.

(A) 107(1→2). Cervical pleurocoels present as foramina leading to internal centrum cavities.

(A) 123(1→0). Neural spines of post-axial cervicals dorsoventrally high.

(A) 153(1→0). Sacral ribs and transverse processes remain separate from ilia in adults.

(A) 158(1→2). Neural arch elements (transverse processes, neural spines) reduced in mid-caudal vertebrae.

(A) 202. Pubic peduncle of ilium projects ventrally much further than ischial peduncle.

(A) 207(1→0). Axis of pubic shaft straight.

(A) 233(1→2). Fibular crest (=crista fibularis) of tibia distally placed, flange-like, separated from proximal tibia.

(A) 262. Metatarsal V shaft mediolaterally flattened and distal end angles dorsally (anteriorly).

(D) 34(0→2). Promaxillary fenestra of maxilla present and concealed from lateral view by lateral lamina of maxillary antorbital fossa.

(D) 82. Ventral edge of proximal end of paroccipital process at same level or ventral to horizontal plane through middle of occipital condyle.

(D) 107(0→2). Cervical pleurocoels present as foramina leading to internal centrum cavities.

(D) 110(1→3). Cervical epipophyses strongly developed, and project mostly dorsally above zygapophyses.

(D) 133. Cervical rib heads marked by pneumatic excavations.

(D) 136. Anterior dorsal vertebrae with pleurocoel in anterior half of centrum.

(D) 143. Neural spines of posterior dorsal vertebrae substantially taller than anteroposteriorly long.

(D) 162. Furcula (=median fusion of clavicles) present.

(D) 168. Posteroventral process of coracoid expanded beyond margin of glenoid fossa.

(D) 183. Manual digit II is longest of the manus.

(D) 194. Ventral rim of preacetabular process of ilium with ventral expansion or 'hook'.

(D) 200. Pubic peduncle of ilium size much greater than ischial peduncle.

(D) 208. Medial lamina of pubis stops short of distal tip of pubic shaft, resulting in short median separation between distal tips of pubes.

(D) 233(0→2). Fibular crest (=crista fibularis) of tibia distally placed, flange-like, separated from proximal tibia.

(D) 236(1→2). Tibia distal profile subtriangular with large posterolateral expansion.

(D) 247. Ascending process of astragalus anteroposteriorly flattened.

Ceratosauria (node diagnosed = *Coelophysis* + *Carnotaurus*)

Unambiguous apomorphies:

106. Posterior pleurocoels in post-axial cervical centra.

118. Anterodorsal border of axial neural spine dorsally convex and blade-like

119. Axial neural spine extends anteriorly beyond prezygapophyses.

131. Cervical ribs exceptionally thin posteriorly (styliform).

139. Dorsal transverse processes with strongly backswept anterior margin resulting in triangular profile in dorsal view.
140. Transverse processes of dorsal vertebrae broad, extending to lateral margin of prezygapophysis.
150. Sacral centra exhibit full fusion to one another so sutures nearly indiscernible by adulthood.
151. Sacral neural arch elements (transverse processes, arches, neural spines) and sacral ribs of adjacent vertebrae fuse to one another by adulthood.
152. Sacral transverse process of at least mid-sacrals coalesce to form nearly continuous horizontal sheet in dorsal view by adulthood.
167. Anterior margin of scapulocoracoid at scapula-coracoid contact continuous and uninterrupted in adults.
189. Pelvic bones co-ossify with one another by adulthood.
191. Dorsal margin of ilium linear/angular.
196. Brevis fossa of ilium very broad posteriorly.
221. Femoral dimorphism present, expressed in muscle scars, attachments, and processes ('robust' versus 'gracile' morphs).
227. Tibiofibular crest of femur sharply demarcated from lateral distal condyle by sulcus or concavity.
228. Femoral popliteal fossa traversed by infrapopliteal ridge between medial (=tibial) distal condyle and tibiofibular crest in adults.
249. Astragalus and calcaneum fuse to each other by adulthood.

Ambiguous apomorphies:

(A) 45. Frontals anteroposteriorly elongated and triangular in dorsal view.

(A) 58. Lateral lamina of lacrimal ventral ramus sinuous and protrudes anteriorly beyond medial lamina.

(A) 74. Quadratojugal and quadrate fuse in adults.

(A) 92. Splenial posterior margin straight, not forked.

(A) 130. Cervical ribs co-ossify to their respective vertebral centra in adults.

(A) 141. Posterior dorsal vertebral centrum length ≥1.33 times height of anterior articular surface.

(A) 154. Ventral surface of caudal centra bear narrow, sharp longitudinal groove.

(A) 159(2→1). Distal caudal vertebral zygapophyses with 25%<50% overlap of preceding centrum.

(A) 165. Posterior margin of scapular blade nearly straight over most of length, curves posteriorly only at distal tip.

(A) 195. Supraacetabular crest of ilium flares lateroventrally to form hood-like overhang that hides anterodorsal half of acetabulum in lateral view.

(A) 198. Posterior margin of ilium posteriorly concave, notched, or indentated in lateral view.

(A) 214. Ischial antitrochanter large and protrudes anterolaterally into acetabulum, giving 'notched' profile to posteroventral margin of acetabulum.

(A) 217(1→2). Distal tip of ischium >3 times minimum anteroposterior width of ischial shaft.

(A) 238. Medial side of proximal end of fibula with oblique (posteroproximal to anterodistal) ridge that overlaps proximal part of medial fibular groove.

(A) 260. Proximal end of metatarsal III with ventral boss protruding beyond plane of metatarsal shafts.

(D) 12. Maxillary process of premaxilla does not contact nasal, allowing maxilla to contribute to rim of external naris.

(D) 34. Promaxillary fenestra of maxilla present, clearly visible in lateral view.

(D) 107. Cervical pleurocoels present as deep ovoid fossae or pockets.

(D) 153. Sacral ribs and transverse processes fuse to ilia in adults.

(D) 161. Anterior processes on proximal end of haemal arches (chevrons) are small tubercules.

(D) 207. Axis of pubic shaft curves ventrally, resulting in anterior bowing (convex anterior, concave posterior) of shaft in lateral view.

(D) 233. Fibular crest (=crista fibularis) of tibia a low ridge extending distally from proximal tibia.

Ceratosauroidea (node diagnosed = *Elaphrosaurus* + *Carnotaurus*)

Unambiguous apomorphies:

144. Vertebra 23 incorporated into sacral series (as dorsosacral 3).

148. Ventral margin of sacral series exhibits strong dorsal-ward arching.

171. Humerus straight in lateral view.

204. Ilium-pubis articulation deep peg-in-socket (socket in pubis) connection.

259. Proximal end of metatarsal III backs metatarsals II and IV ventrally, resulting in "T"-shaped proximal profile ("antarctometatarsus").

Ambiguous apomorphies:

(A) 6. Premaxilla body (excludes maxillary and nasal processes) height/length ratio >1.25.

(A) 13. Maxillary process of premaxilla anteroposterior length much < length of alveolar body of premaxilla.

(A) 15. Palatal process of premaxilla only a blunt ridge or absent.

(A) 39. Nasals partially fused, at anterior end or within median crests or prominences.

(A) 43(1→2). Lateral surface of anterior end of nasal along margin of external naris with laterally convex hood covering posterior part of external naris.

(A) 67. Jugal-maxilla overlap length ≥50% total jugal length.

(A) 75. Quadrate tall and posteroventrally angled so ventral condyle is posterior to dorsal condyle and paraoccipital processes.

(A) 76. Quadrate foramen absent.

(A) 77. Supratemporal fossae in contact posteriorly but separated anteriorly by triangular plate of parietals.

(A) 83. Interorbital braincase elements (i.e., interorbital septum or mesethmoid, orbitosphenoid, sphenethmoid) ossify by adulthood.

(A) 89. Posteroventral process of dentary subequal in length to posterodorsal process.

(A) 96(1→2). Mesial premaxillary teeth cross-section asymmetrical, "D"-shaped.

(A) 98. Maxillary interdental plates fuse to each other.

(A) 108(0→2). Internal pneumatic cavities in vertebral centra present with camellate structure.

(A) 120. Axial neural arch with pneumatic foramen/foramina posterodorsal to diapophysis.

(A) 121. Anterior post-axial cervical centra with median ventral keel.

(A) 136(1→0). Anterior dorsal vertebrae without pleurocoel in anterior half of centrum.

(A) 162(1→0). 162. Furcula (=median fusion of clavicles) absent.

(A) 166. Anterodorsal border of acromion process of scapula has smooth, continuous, high-angle transition to scapular blade.

(A) 170. Humerus proximal head rounded, bulbous, subspherical.

(A) 173. Humeral distal condyles flattened.

(A) 174(0→2). Deltopectoral crest small, only a low triangular eminence.

(A) 175. Radius length < 50% humerus length.

(A) 177(1→0). Distal carpals I and II separate.

(A) 182(1→0). Phalanx I-1 length/metacarpal I length ≤1.0.

(A) 183(1→0). Manual digit III (0), or manual digit II.

(A) 190. Ilium anteroposterior length about as long or longer than femur.

(A) 208(1→0). Medial lamina of pubis that reaches distal tip of shaft.

(A) 211. Distal expansion of pubis medially inset from lateral edge of pubic shaft.

(A) 264. Ungual of pedal digit II asymmetrical.

(D) 198. Posterior margin of ilium posteriorly concave, notched, or indentated in lateral view.

(D) 200. Pubic peduncle of ilium size much greater than ischial peduncle.

(D) 217(1→2). Distal tip of ischium >3 times minimum anteroposterior width of ischial shaft.

(D) 236(1→2). Tibia distal profile subtriangular with large posterolateral expansion.

(D) 260. Proximal end of metatarsal III with ventral boss protruding beyond plane of metatarsal shafts.

Neoceratosauria (=*Ceratosaurus* + *Carnotaurus*)

Unambiguous apomorphies:

137. Dorsal vertebrae with parapophyses that project laterally on "stalks".

172(1→0). Humerus shaft torsion absent.

229. Anteroposterior length of cnemial crest of tibia ≥ width across proximal (=femoral) condyles of tibia.

239(1→2). Fibular M. iliofibularis insertion large anterolaterally projecting tubercule or process.

250. Astragalus and tibia fuse to each other by adulthood.

251(1→2). Calcaneum with large tibial facet covering most of posterior surface and reaches nearly to lateral edge of calcaneum.

Ambiguous apomorphies:

(A) 107(1→2). Cervical pleurocoels present as foramina leading to internal centrum cavities.

(A) 141(1→0). Posterior dorsal vertebral centrum length <1.33 times height of anterior articular surface.

(A) 149. Diameter of mid-sacral centra substantially smaller than posterior dorsals and anterior caudals.

(A) 157. Neural spines of mid-caudal vertebrae tall, rod-like, and vertically directed.

(A) 176. Radius and ulna distal articular surfaces large and subhemispherical.

(A) 195(1→0). Supraacetabular crest of ilium a weakly developed ridge or raised shelf.

(D) 6. Premaxilla body (excludes maxillary and nasal processes) height/length ratio >1.25.

(D) 13. Maxillary process of premaxilla anteroposterior length much < length of alveolar body of premaxilla.

(D) 15. Palatal process of premaxilla only a blunt ridge or absent.

(D) 43(1→2). Lateral surface of anterior end of nasal along margin of external naris with laterally convex hood covering posterior part of external naris

(D) 66. Anterior process of postorbital at about same level as posterior process, resulting in T-shaped postorbital.

(D) 67. Jugal-maxilla overlap length ≥50% total jugal length.

(D) 75. Quadrate tall and posteroventrally angled so ventral condyle is posterior to dorsal condyle and paraoccipital processes.

(D) 76. Quadrate foramen absent.

(D) 77. Supratemporal fossae in contact posteriorly but separated anteriorly by triangular plate of parietals.

(D) 82. Ventral edge of proximal end of paroccipital process at same level or ventral to horizontal plane through middle of occipital condyle.

(D) 83. Interorbital braincase elements (i.e., interorbital septum or mesethmoid, orbitosphenoid, sphenethmoid) ossify by adulthood.

(D) 84. Ectopterygoid flange of pterygoid marked by fossa.

(D) 96(0→2). Mesial premaxillary teeth cross-section asymmetrical, "D"-shaped.

(D) 98. Maxillary interdental plates fuse to each other.

(D) 107(1→2). Cervical pleurocoels present as foramina leading to internal centrum cavities.

(D) 110(1→3). Cervical epipophyses strongly developed, and project mostly dorsally above zygapophyses.

(D) 114. Axis bears pleurocoels.

(D) 120. Axial neural arch with pneumatic foramen/foramina posterodorsal to diapophysis.

(D) 133. Cervical rib heads marked by pneumatic excavations.

(D) 143. Neural spines of posterior dorsal vertebrae substantially taller than anteroposteriorly long.

(D) 154. Ventral surfaces of caudal centra bear narrow, sharp longitudinal groove.

(D) 164. Distal end of scapular blade not expanded.

(D) 166. Anterodorsal border of acromion process of scapula has smooth, continuous, high-angle transition to scapular blade.

(D) 190. Ilium anteroposterior about as long or longer than femur.

(D) 194. Ventral rim of preacetabular process of ilium with ventral expansion or 'hook'.

(D) 216. Obturator process of ischium distally separated from ischial shaft by notch.

(D) 247. Ascending process of astragalus anteroposteriorly flattened.

Abelisauria (=*Noasaurus* + *Carnotaurus*)

Unambiguous apomorphies:

21(0→2). Dorsal process of maxilla axis angles posterodorsally >50º from horizontal.

88. Posterodorsal end of dentary with socket for surangular prong.

90. External mandibular fenestra very large.

112. Cervical epipophyses at level dorsal to top of neural spine.

113. Cervical vertebrae with epipophyseal-prezygapophyseal laminae.

124. Neural spines of post-axial cervicals anteroposteriorly very short.

125. Cervical zygapophyses positioned far laterally away from centrum in dorsal view.

126. Post-axial cervical neural arches house pneumatic cavities lateral to neural canal.

127. Lateral surface of post-axial cervical arch pedicels pierced by foramen/foramina anteroventral to postzygapophysis.

134. Anterior cervical rib shafts proximal part greatly expanded and flattened.

135. Cervical and dorsal neural arch surfaces ventral to transverse processes pierced by multiple pneumatic foramina.

225(1→2). Medial epicondyle of femur hypertophied and flange-like.

242. Fibula co-ossifies with ascending process of astragalus of adults.

263. Pedal unguals with two lateral grooves.

Ambiguous apomorphies:

(A) 8. Premaxilla nasal process comprises ≤ 50% of external naris anterodorsal border.

(A) 22. Dorsal process of maxilla with very short posterior component that does not contact lacrimal.

(A) 39. Nasals fused over entire length in adults.

(A) 41. Dorsal surfaces of nasals rugose, with heavy pitting and sculpturing.

(A) 42. Lateral or posterolateral surface of nasal perforated by pneumatic foramen/foramina.

(A) 45(1→0) Frontals anteroposteriorly short and approximately rectangular.

(A) 46. Frontals indistinguishably fuse to each other in adults.

(A) 48. Frontals and parietals fuse in adults.

(A) 50. Dorsal surface of parietal with transversely thickened sagittal crest between supratemporal fenestrae.

(A) 51. Parietal nuchal crest greatly enlarged and elevated.

(A) 54. Anterior ramus of lacrimal dorsoventral height much narrower than anteroposterior width of ventral ramus of lacrimal.

(A) 55. Ratio of lacrimal anterior ramus length versus ventral ramus length < 0.65.

(A) 56. Lacrimal bears posterior process that contacts postorbital, excluding frontal from rim of orbit.

(A) 58(1→0). Lateral lamina of lacrimal ventral ramus linear and remains posterior to medial lamina.

(A) 59(1→0). Lacrimal antorbital fossa small or nonexistent.

(A) 61. Lacrimal ventral process with suborbital process/posterior convexity.

(A) 63. Ventral (=jugal) process of postorbital with distinct suborbital process.

(A) 68. Anterior process of jugal bears dorsal flange that laterally overlaps ventral process of lacrimal.

(A) 70(2→1). Posterior process of jugal divided, ventral prong subequal or much shorter than dorsal prong.

(A) 73(0→2). Quadratojugal and squamosal contact absent.

(A) 130(1→0). Cervical ribs remain separate from their respective vertebral centra in adults.

(A) 139(1→0). Dorsal transverse processes directed laterally, giving rectangular profile in dorsal view.

(A) 152(1→0). Sacral transverse process of at least mid-sacrals remain separate in adulthood.

(A) 169. Humerus length <1/3 femur length.

(A) 178(1→0). Distal ends of metacarpals dorsally rounded, smooth.

(A) 179. Manual digit I reduced to sub-conical, blocky metacarpal that lacks distal articular condyles and phalanges.

(A) 181(1→0). Metacarpal I with symmetrical distal articular condyles.

(A) 214(1→0). Ischial antitrochanter small, indistinct.

(A) 238(1→0). Medial side of proximal end of fibula flat.

(D) 89. Posteroventral process of dentary subequal in length to posterodorsal process.

(D) 123. Neural spines of post-axial cervicals dorsoventrally low.

(D) 170. Humerus proximal head rounded, bulbous, subspherical.

(D) 174(0→2). Deltopectoral crest a small, only a low triangular eminence.

(D) 211. Distal expansion of pubis medially inset from lateral edge of pubic shaft.

(D) 244. Ascending process of astragalus height ≥ (1) height of main body of astragalus.

Noasauridae (node diagnosed = *Noasaurus* + *Masiakasaurus*)

Unambiguous apomorphies:

28. Maxilla with ≤10 teeth/alveoli in adults.

34(1→0). Promaxillary fenestra of maxilla absent.

38(1→0). Medial surface of anteromedial process of maxilla smooth.

129. Cervical neural spines positioned mostly over anterior half of centrum.

142. Posterior dorsal vertebral centrum length ≥2 times height of anterior articular surface.

258. Mediolateral width of metatarsal II shaft < width of IV and both < III.

Ambiguous apomorphies:

(A) 18(1→0). Premaxilla-maxilla suture uninterrupted, no subnarial foramen.

(A) 23(1→0). Anterior process of maxilla length ≤10% total maxilla length.

(A) 26. Maxillary first alveolus opens anteroventrally.

(A) 91(1→0). Splenial without foramen (either closed or ventrally open) near anteroventral margin.

(A) 92(1→0). Splenial posterior margin forked.

(A) 100. Maxillary interdental plates low and partially obscured by lamina of maxilla in medial view.

(A) 101. Mesial dentary teeth enlarged relative to mid- and distal dentary teeth.

(A) 108(2→1). Internal pneumatic cavities in vertebral centra present with camerate structure.

(A) 141. Posterior dorsal vertebral centrum length ≥1.33 times height of anterior articular surface.

(A) 148(1→0). Ventral margin of sacral series relatively straight.

(A) 149(1→0). Diameter of mid-sacral centra approximately the same as posterior dorsals and anterior caudals.

(A) 157(1→0). Neural spines of mid-caudal vertebrae rod-like and posteriorly inclined.

(A) 189(1→0). Pelvic bones remain separate in adulthood.

(A) 210(2→1). Distal tip of pubis enlarged 2<3 times anteroposterior width of pubic shaft.

(A) 223. Femoral anterior trochanter reaches proximally at least to mid-point of femoral head.

(A) 228(1→0). Femoral popliteal fossa smooth in adults.

(D) 141. Posterior dorsal vertebral centrum length ≥1.33 times height of anterior articular surface.

***Xenotarsosaurus* + *Carnotaurus* clade**

Unambiguous apomorphies:

136. Anterior dorsal vertebrae with pleurocoel in anterior half of centrum.

Ambiguous apomorphies:

(A) 1. Craniofacial bones (i.e., maxilla, jugal, quadratojugal, nasal) sculptured.

(A) 31. Maxillary antorbital fossa anterior to internal antorbital fenestra narrow, extends little beyond rim of internal antorbital fenestra.

(A) 33. Maxillary antorbital fossa ventral to internal antorbital fenestra very narrow or obscured in lateral view.

(A) 99. Medial surfaces of maxillary interdental plates heavily striated/ridged.

(A) 122. Post-axial cervical prespinal fossae broad.

(A) 155. Distal ends of transverse processes of anterior caudal vertebrae anteroposteriorly expanded.

(A) 207(1→0) Axis of pubic shaft straight.

(A) 208. Medial lamina of pubis stops short of distal tip of pubic shaft, resulting in short median separation between distal tips of pubes.

***Ilokelesia* + *Carnotaurus* clade**

Unambiguous apomorphies: none.

Ambiguous apomorphies:

(A) 220(1→0). Femoral head relatively continuous with posterior surface of femur.

(A) 232. Anterior tip of cnemial crest of tibia proximodistally expanded.

(D) 56. Lacrimal bears posterior process that contacts postorbital, excluding frontal from rim of orbit.

(D) 63. Ventral (=jugal) process of postorbital with distinct suborbital process.

(D) 122. Post-axial cervical prespinal fossae broad.

(D) 139(1→0). Dorsal transverse processes directed laterally, giving rectangular profile in dorsal view.

(D) 264. Ungual of pedal digit II asymmetrical.

Abelisauridae (=*Abelisaurus* + *Carnotaurus*)

Unambiguous apomorphies:

62 (Postorbital long-axis or) 1 0.500 0 ==> 1

Ambiguous apomorphies:

(A) 65. Postorbital with stepped-down ventrolateral fossa.

(D) 1. Craniofacial bones (i.e., maxilla, jugal, quadratojugal, nasal) sculptured.

(D) 22. Dorsal process of maxilla with very short posterior component that does not contact lacrimal.

(D) 31. Maxillary antorbital fossa anterior to internal antorbital fenestra narrow, extends little beyond rim of internal antorbital fenestra.

(D) 33. Maxillary antorbital fossa ventral to internal antorbital fenestra very narrow or obscured in lateral view.

(D) 39(0→2). Nasals fused over entire length in adults.

(D) 41. Dorsal surfaces of nasals rugose, with heavy pitting and sculpturing.

(D) 42. Lateral or posterolateral surface of nasal perforated by pneumatic foramen/foramina.

(D) 46. Frontals indistinguishably fuse to each other in adults.

(D) 48. Frontals and parietals fuse in adults.

(D) 50. Dorsal surface of parietal with transversely thickened sagittal crest between supratemporal fenestrae.

(D) 51. Parietal nuchal crest greatly enlarged and elevated.

(D) 59(1→0). Lacrimal antorbital fossa small or nonexistent.

(D) 61. Lacrimal ventral process with suborbital process/posterior convexity.

***Majungatholus* + *Carnotaurus* clade**

Unambiguous apomorphies:

47. Frontals contribute to dorsal skull roof prominences (i.e. horns, knobs, bosses).

49. Frontal-parietal contact area with median fossa in saddle-shaped depression.

Ambiguous apomorphies:

(D) 54. Anterior ramus of lacrimal dorsoventral height much narrower than anteroposterior width of ventral ramus of lacrimal.

(D) 55. Ratio of lacrimal anterior ramus length versus ventral ramus length < 0.65.

(D) 65. Postorbital with stepped-down ventrolateral fossa.

(D) 68. Anterior process of jugal bears dorsal flange that laterally overlaps ventral process of lacrimal.

(D) 70(2→1). Posterior process of jugal divided into subequal dorsal and ventral prongs.

(D) 94. Retroarticular process of mandible much broader than mandible anterior to jaw joint.

(D) 108(0→2). Internal pneumatic cavities in vertebral centra present with camellate structure.

(D) 121. Anterior post-axial cervical centra with median ventral keel.

(D) 149. Diameter of mid-sacral centra substantially smaller than posterior dorsals and anterior caudals.

(D) 168. Posteroventral process of coracoid expanded beyond margin of glenoid fossa.

(D) 169. Humerus length <1/3 (1) femur length.

(D) 232. Anterior tip of cnemial crest of tibia proximodistally expanded.

***Aucasaurus* + *Carnotaurus* clade**

Unambiguous apomorphies:

47(1→2). Frontals bear large, laterally positioned supraorbital horns.

111. Cervical epipophyses with anteriorly directed processes.

156. Hyposphene-hypantrum articulations present on anterior and mid-caudal vertebral arches.

Ambiguous apomorphies:

(A) 23(1→0). Anterior process of maxilla length ≤10% total maxilla length.

(A) 242(1→0). Fibula separate from ascending process of astragalus of adults.

(D) 155. Distal ends of transverse processes of anterior caudal vertebrae anteroposteriorly expanded.

(D) 165. Posterior margin of scapular blade nearly straight over most of length, curves posteriorly only at distal tip.

(D) 175. Radius length < 50% humerus length.

(D) 176. Radius and ulna distal articular surfaces large and subhemispherical.

(D) 178(1→0). Distal ends of metacarpals dorsally rounded, smooth.

(D) 179. Manual digit I reduced to sub-conical, blocky metacarpal that lacks distal articular condyles and phalanges.

(D) 181(1→0). Metacarpal I with symmetrical distal articular condyles.

(D) 207(1→0). Axis of pubic shaft straight.

(D) 210(1→2). Distal tip of pubis ≥3 times anteroposterior width of pubic shaft.

Coelophysoidea (node diagnosed = *Dilophosaurus* + *Coelophysis*)

Unambiguous apomorphies:

2. Skull length >3 times posterior skull height (height = articular condyle of quadrate to dorsal-most edge of parietal)

5. Internal antorbital fenestra anteroposterior length ≥ 25% maximum skull length.

9. Premaxillary tooth row terminates entirely anterior to external naris.

14. Maxillary process of premaxilla ventral margin with posteroventrally directed flange, resulting in appearance of "forked" premaxilla.

16. Premaxilla and maxilla only loosely articulated with each other.

17. Premaxilla and maxilla alveolar margins do not contact.

25. Anterior tip of maxillary alveolar margin curves sharply mediodorsally.

26. Maxillary first alveolus opens anteroventrally.

37. Anteromedial process of maxilla is long, finger-like projection.

86. Dorsal edge of anterior tip of dentary raised conspicuously relative to middle and posterior parts of dentary.

95. Serrations on mesial-most premaxillary teeth are very small and few in number, or wholly lacking.

101. Mesial dentary teeth enlarged relative to mid- and distal dentary teeth.

110(3→2). Cervical epipophyses elongate, narrow, and project posterolaterally beyond postzygapophyses.

115. Axis lacks a distinct diapophysis.

116. Axial parapophysis weakly developed to indiscernible.

203. Pubic peduncle of ilium with two facets separated by kink, resulting in anterior and ventral-oriented pubic contacts.

209. Distal tips of pubes without median contact.

222(2→1). Femoral anterior trochanter a conical spike or pyramidal prominence.

<u>Ambiguous apomorphies</u>:

(A) 40(0→2). Lateral margin of nasal forms part of parasagittal crest rising from dorsolateral margin of skull.

(A) 66(1→0). Anterior process of postorbital dorsally higher than posterior process.

(A) 82(1→0). Ventral edge of proximal end of paroccipital process is dorsal to horizontal plane through middle of occipital condyle.

(A) 84(1→0). Ectopterygoid flange of pterygoid flat.

(A) 85. Ectopterygoid ventral surface with deep fossa.

(A) 94(1→0). Retroarticular process of mandible about same mediolateral width as mandible anterior to jaw joint.

(A) 114(1→0). Axis lacks pleurocoels.

(A) 132. Cervical ribs ≥4 times centrum length.

(A) 133(1→0). Cervical rib heads without signs of pneumaticity.

(A) 164(1→0). Distal end of scapular blade markedly expanded.

(A) 168(1→0). Posteroventral process of coracoid not expanded beyond glenoid fossa.

(A) 194(1→0). Ventral rim of preacetabular process of ilium relatively horizontal.

(A) 200(1→0). Pubic peduncle of ilium size approximately equal to ischial peduncle.

(A) 210(2→1). Distal tip of pubis enlarged 2<3 times anteroposterior width of pubic shaft.

(A) 213. Ischium length ≤2/3 the length of pubis.

(A) 236(2→1). Tibia distal profile subrectangular with small posterolateral extension.

(A) 247(1→0). Ascending process of astragalus robust, pyramidal prominence.

(A) 252. Distal tarsal III fuses to metatarsal III by adulthood.

(A) 257. Proximal ends of metatarsals II and III co-ossify to each other by adulthood.

(D) 8(1→0). Premaxilla nasal process comprises > 50% of external naris anterodorsal border.

(D) 45. Frontals anteroposteriorly elongated and triangular in dorsal view.

(D) 58. Lateral lamina of lacrimal ventral ramus sinuous and protrudes anteriorly beyond medial lamina.

(D) 136. Anterior dorsal vertebrae with pleurocoel in anterior half of centrum.

(D) 141. Posterior dorsal vertebral centrum length ≥1.33 times height of anterior articular surface.

(D) 154. Ventral surface of caudal centra bear narrow, sharp longitudinal groove.

(D) 165. Posterior margin of scapular blade nearly straight over most of length, curves posteriorly only at distal tip.

(D) 177. Distal carpals I and II fuse to each other, resulting in single element proximally capping metacarpals I and II.

(D) 182. Phalanx I-1 length/metacarpal I length >1.0.

(D) 183. Manual digit II is longest of the manus.

(D) 195. Supraacetabular crest of ilium flares lateroventrally to form hood-like overhang that hides anterodorsal half of acetabulum in lateral view.

(D) 208. Medial lamina of pubis stops short of distal tip of pubic shaft, resulting in short median separation between distal tips of pubes.

(D) 214. Ischial antitrochanter large and protrudes anterolaterally into acetabulum, giving 'notched' profile to posteroventral margin of acetabulum.

(D) 216. Obturator process of ischium distally separated from ischial shaft by notch.

(D) 238. Medial side of proximal end of fibula with oblique (posteroproximal to anterodistal) ridge that overlaps proximal part of medial fibular groove.

***Liliensternus* + *Coelophysis* clade**

Unambiguous apomorphies:

30. Ventral margin of maxillary antorbital fossa sharply marked by alveolar ridge that parallels alveolar margin.

Ambiguous apomorphies:

(A) 7. Premaxilla lateral surface with few or no neurovascular foramina.

(A) 10. Premaxillary lateral surface dorsal to second tooth position marked by small pit at base of nasal process.

(A) 23(1→0). Anterior process of maxilla length ≤10% total maxilla length.

(A) 27. Maxilla with ≥20 teeth/alveoli in adults.

(A) 32. Anterior margin of maxillary antorbital fossa squared, with angular corners and nearly straight anterior border.

(A) 38(1→0). Medial surface of anteromedial process of maxilla smooth.

(A) 40(2→3). Lateral margins of nasals form all of thin parasagittal crests.

(A) 55(0→2). Ratio of lacrimal anterior ramus length versus ventral ramus length >1.00.

(A) 80. Transverse intertuberal lamina of basisphenoid bears small median spur that projects anteriorly along roof of basisphenoidal recess.

(A) 93. Angular reaches posterior end of mandible, blocking surangular from ventral margin of jaw in lateral view.

(A) 97. Long axis of mesial premaxillary teeth nearly straight.

(A) 126. Post-axial cervical neural arches house pneumatic cavities lateral to neural canal.

(A) 143(1→0). Neural spines of posterior dorsal vertebrae no taller than anteroposteriorly long.

(A) 217(2→1). Distal tip of ischium enlarged ≤3 times minimum anteroposterior width of ischial shaft.

(A) 244(1→0). Ascending process of astragalus height < height of main body of astragalus.

(D) 85. Ectopterygoid ventral surface with deep fossa.

(D) 123. Neural spines of post-axial cervicals dorsoventrally low.

(D) 213. Ischium length ≤2/3 the length of pubis.

(D) 260. Proximal end of metatarsal III with ventral boss protruding beyond plane of metatarsal shafts.

***Zupaysaurus* + *Coelophysis* clade**

Unambiguous apomorphies: none.

Ambiguous apomorphies:

(A) 127(0→2). Lateral surface of post-axial cervical arch pedicels bear triangular, posterior-directed apertures anterior to postzygapophysis.

(A) 128. Mid-cervical centrum length 3<4 times diameter of anterior face.

(A) 142. Posterior dorsal vertebral centrum length ≥2 times height of anterior articular surface.

(A) 199. Ilium with M. iliofemoralis fossa that stops short of bone's posterior margin, resulting in distinct rim on lateral surface of postacetabular process.

(D) 23(1→0). Anterior process of maxilla length ≤10% total maxilla length.

(D) 27. Maxilla with ≥20 (1) teeth/alveoli in adults.

(D) 32. Anterior margin of maxillary antorbital fossa squared, with angular corners and nearly straight anterior border.

(D) 40(0→3). Lateral margins of nasals form all of thin parasagittal crests.

(D) 55(0→2). Ratio of lacrimal anterior ramus length versus ventral ramus length >1.00.

(D) 130. Cervical ribs co-ossify to their respective vertebral centra in adults.

Shake-N-Bake taxon + *Coelophysis* clade

Unambiguous apomorphies:

241. Fibula bears medial flange that overlaps part of the ascending process of astragalus.

243(1→2). Fibular facet on proximal surface of astragalus a small subtriangular fossa on anterolateral corner of proximal surface of astragalus.

250. Astragalus and tibia fuse to each other by adulthood.

Ambiguous apomorphies:

(A) 3(1→0). Orbit approximately circular.

(A) 69. Jugal does not contact internal antorbital fenestra, participates in external antorbital fenestra.

(A) 71. Lateral surface of jugal with low rounded ridge that traverses anterior and posterior processes.

(A) 72(1→0). Ventral process of squamosal narrow.

(A) 74(1→0). Quadratojugal and quadrate fuse in adults.

(A) 89. Posteroventral process of dentary subequal in length to posterodorsal process.

(D) 126. Post-axial cervical neural arches house pneumatic cavities lateral to neural canal.

(D) 127(0→2). Lateral surface of post-axial cervical arch pedicels bear triangular, posterior-directed apertures anterior to postzygapophysis.

(D) 128. Mid-cervical centrum length 3<4 times diameter of anterior face.

(D) 142. Posterior dorsal vertebral centrum ≥2 times height of anterior articular surface.

(D) 199. Ilium with M. iliofemoralis fossa that stops short of bone's posterior margin, resulting in distinct rim on lateral surface of postacetabular process.

(D) 252. Distal tarsal III fuses to metatarsal III by adulthood.

(D) 257. Proximal ends of metatarsals II and III co-ossify to each other by adulthood.

***"Syntarsus" kayentakatae* + *Coelophysis* clade** (="Coelophysidae" advocated)

Unambiguous apomorphies: none

Ambiguous apomorphies:

(D) 3(1→0). Orbit approximately circular.

(D) 7. Premaxilla lateral surface penetrated by few or no neurovascular foramina.

(D) 38(1→0). Medial surface of anteromedial process of maxilla smooth.

(D) 71. Lateral surface of jugal with low rounded ridge that traverses anterior and posterior processes.

(D) 72(1→0). Ventral process of squamosal narrow.

(D) 80. Transverse intertuberal lamina of basisphenoid bears small median spur that projects anteriorly along roof of basisphenoidal recess.

(D) 96. Mesial premaxillary teeth cross-section subcircular.

(D) 97. Long axis of mesial premaxillary teeth nearly straight.

(D) 132. Cervical ribs ≥4 times centrum length.

(D) 162. Furcula (=median fusion of clavicles) present.

(D) 198. Posterior margin of ilium posteriorly concave, notched, or indentated in lateral view.

***"Syntarsus" kayentakatae* + *Segisaurus* clade**

Unambiguous apomorphies:

166. Anterodorsal border of acromion process of scapula has smooth, continuous, high-angle transition to scapular blade.

212(1→0). Distal tip of pubis elongate rectangular or subequant.

Ambiguous apomorphies:

(A) 20. Transition along dorsal border of maxilla from anterior process to dorsal process abrupt to angular in lateral view.

(A) 24(1→0). Ratio of dorsoventral height of proximal end of anterior process of maxilla versus height of alveolar ramus of maxilla at first alveolus posterior to rim of internal antorbital fenestra <1.0.

(A) 82. Ventral edge of proximal end of paroccipital process at same level or ventral to horizontal plane through middle of occipital condyle.

(A) 187(1→0). Manual digit IV with >1 phalanx.

***Syntarsus rhodesiensis* + *Coelophysis* clade** (= strictly interpreted "Coelophysidae")

Unambiguous apomorphies:

21. Dorsal process of maxilla axis angles posterodorsally ≤ 35º from horizontal.

34(1→0). Promaxillary fenestra of maxilla absent.

40(3→1). Lateral margin of nasal bears low expanded ridge.

58(1→0). Lateral lamina of lacrimal ventral ramus linear and remains posterior to medial lamina.

87. Dentary tooth count >18.

Ambiguous apomorphies:

(A) 69(1→2). Jugal with no participation in external antorbital fenestra.

(A) 93(1→0). Angular stops short of posterior end of mandible.

(A) 259. Proximal end of metatarsal III backs metatarsals II and IV ventrally, resulting in "T"-shaped proximal profile ("antarctometatarsus").

(D) 69(0→2). Jugal with no participation in external antorbital fenestra.

Discussion

The results of my analysis retrieved a monophletic Ceratosauria that included the coelophysoid theropods, findings consistent with the hypotheses obtained by Gauthier (1986), Rowe (1989), Rowe and Gauthier (1990), Holtz (1998), Sereno (1999a), and followed by Padian et al. (1999). The results do not agree with recent works that found Ceratosauria sensu Rowe (1989) was a paraphyletic assemblage of basal theropod taxa (Forster, 1999; Carrano and Sampson, 1999; Carrano et al., 2002; Rauhut, 2003; Wilson

et al., 2003; Sereno et al., 2004). These differences can probably be attributed to two factors. The first is a combination of new data and reinterpretation of morphologies and character states in many coelophysoid taxa. The second factor is recognition of the limitations placed upon coding character states in coelophysoid taxa to reflect the maturity of pertinent fossil specimens, and treating relevant characters as missing data in taxa not represented by adequately mature specimens.

Phylogeny and geologic time - Figure 109 depicts the cladogram shown in Figure 108D (one of 1050 equally most parsimonious trees generated by phylogenetic test 3), superimposed upon the geologic time scale (Gradstein et al., 2005). Heavy lines in Figure 109 indicate the estimated temporal range of each taxon. The filled circles on the heavy lines indicate either mid-range or 'best guess' of each taxon's distribution within their broader temporal range. Dashed branches in subsequent figures represent uncertain or equivocal position of taxa relative to other theropods, based mainly upon a reasonable estimate of the taxon's phylogenetic position in an Adams consensus cladogram. The same conventions are used in all the subsequent figures that depict the phyogeny of theropod taxa superimposed on the geologic time scale. Estimates and assignments for the temporal distribution of taxa were derived from Gilmore (1920), Janensch (1925), Camp (1936), Welles (1954, 1984), Raath (1969, 1977), Madsen (1976), Galton and Jensen (1979), Colbert (1981, 1989), Olsen and Galton (1984), Clark and Fastovsky (1986), Olsen and Sues (1986), Sereno and Arcucci (1994), Charig and Milner (1997), Sampson et al. (1998), Sereno et al. (1998), Rauhut and Hungerbühler (1998), Coria and

Salgado (1998), Madsen and Welles (2000), Pascual et al. (2000), Lamanna et al. (2002), Coria et al., (2002), Carrano et al. (2002), Sues et al. (2002), Allain (2002), Arcucci and Coria (2003), Wilson et al. (2003), Rauhut (2003), Sereno et al. (2004), Holtz et al. (2004), Galton and Upchurch (2004), Norman et al. (2004), Weishampel et al. (2004), and Carrano and Sampson (2004).

A number of features are apparent when examining the distribution of taxa in relation to their phylogenetic and geologic position. Most noticeable are the long branch uniting the earliest coelophysoids with the earliest ceratosauroids, and the long branch connecting the earliest ceratosaurs with the earliest tetanurans in the analysis. These long lineages can be interpreted as useful predictive tools that highlight likely areas of future discovery. They may also be interpreted as possible evidence against the sister-taxon relationship between Coelophysoidea and Ceratosauroidea, and evidence to support the sister-taxon relationship between Tetanurae and Ceratosauria exclusive of Coelophysoidea.

The lineage connecting basal coelophysoids and basal ceratosauroids spans approximately 60 million years, from early Norian to Kimmeridgian time. This substantial gap in the ceratosaurian record is a legitimate source of concern for any hypothesis that finds these two clades united within Ceratosauria. A number of coelophysoid taxa are present in the fossil record immediately following the coelophysoid-ceratosauroid divergence (Tykoski and Rowe, 2004; Carrano and Sampson, 2004). Fossils of ceratosauroid theropods should also be present in continental sedimentary deposits of Late Triassic, Early Jurassic, and Middle Jurassic age, given the

phylogenetic hypothesis derived from phylogenetic test 3. They should have a worldwide distribution as well, especially given the relative homogeneity of terrestrial vertebrate faunas from deposits of Late Triassic and Early Jurassic time. Yet paleontologists have yet to find an unequivocal ceratosauroid in sediments of these ages.

It may be difficult to recognize a basal ceratosauroid from Late Triassic or Early Jurassic deposits. It can be predicted that a basal ceratosauroid of this age should share many features with basal coelophysoids, being relatively near the divergence between the lineages. For example, the Late Jurassic taxon *Elaphrosaurus bambergi* retains a coelophysoid-like vertebral column (Figs. 40E, 46C) and overall body proportions, which is not surprising given its basal position on the ceratosauroid lineage (Fig. 108A). A basal ceratosauroid should possess few apomorphies in common with derived members of its lineage.

The problematic taxon *Sarcosaurus woodi* is represented by incomplete remains (BMNH 4840/1; an incomplete posterior dorsal vertebra, partial right and left pelvic girdles, and a left femur missing the femoral head and distal condyles) from early Sinemurian age sediments of England (Andrews, 1921; Carrano and Sampson, 2004). *Sarcosaurus* was placed in a basal ceratosaurian polytomy with *Ceratosaurus*, *Segisaurus*, and the coelophysoid lineage in the phylogenetic hypothesis of Rowe and Gauthier (1990), and was considered Ceratosauria *incerte sedis* by Tykoski and Rowe (2004). *Sarcosaurus* was considered a coelophysoid theropod by Carrano and Sampson (2004), although no unambiguously coelophysoid features were listed to place it along that lineage. The femur of *Sarcosaurus* has a pronounced trochanteric shelf, and a simple

subconical or pyramidal anterior trochanter (Andrews, 1921; Carrano and Sampson, 2004), the latter a feature that may be diagnostic of coelophysoids. The pubic peduncle of the ilium might have an anterior-facing articular surface as in coelophysoids, but this is uncertain because of the co-ossification between the ilium and pubis.

In contrast to the low and linear iliac morphology of coelophysoids, the dorsal rim of the iliac blade in *Sarcosaurus* is dorsally arched and strongly convex in lateral view. The preacetabular process of the ilium has a ventral lobe that descends very close to the pubic peduncle of the ilium, a feature not present in coelophysoids (Fig. 69B, C). The ilium of *Sarcosaurus* is similar to that of *Ceratosaurus nasicornis* (Figs. 67B, 74A). The reconstructed length of the ilium (based upon the two partial ilia preserved in the specimen) is approximately the same length as the femur, even accounting for the missing proximal and distal ends of the latter. This resembles the condition in ceratosauroids and tetanurans, whereas the ilium is substantially shorter than the femur in coelophysoids.

The mix of coelophysoid and ceratosauroid features in the femur and pelvis of *Sarcosaurus woodi*, and its presence in Sinemurian age sediments, make it a potential candidate for a basal ceratosauroid. *Sarcosaurus* was added to the taxon-character matrix in phylogenetic test 3 and a test run to find its position on the theropod tree. The strict consensus tree of the 525 equally most parsimonious hypotheses generated placed the taxon as the most basal coelophysoid in the analysis (Fig. 110). Only two unequivocal characters support the placement of *Sarcosaurus* on the coelophysoid lineage. These are the presence of a hood-like supraacetabular crest covering the acetabulum, and a reversal

from an aliform anterior trochanter to a conical or pyramidal anterior trochanter. It would represent a substantial step in closing the temporal gap between the most basal ceratosauroids and coelophysoids if additional material referable to *Sarcosaurus woodi* is found that places the taxon on the ceratosauroid lineage (Fig. 111).

Problematic taxa - Several of the problematic taxa that were excluded from the main phylogenetic analyses can now be evaluated for their geologic, and potential phylogenetic context. The incorporation of these taxa in the initial pre-test analyses resulted in great numbers of equally most parsimonious trees, and great reduction in resolution among the consensus trees (see Chapter 2). However, there remains the chance that these problematic taxa can provide additional information with regard to the relationships and minimum divergence dates among basal theropod lineages.

Camposaurus arizonensis is based upon a pair of distal tibiotarsi (UCMP 34498) with extensive co-ossification between the elements. Several additional coelophysoid-like post-cranial skeletal pieces were also found in the same quarry, but no direct association can be made between them and the type specimens. Only those characters preserved in the type partial tibiotarsi were coded in the taxon-character matrix. The analysis produced 9450 equally most parsimonious hypotheses of phylogeny (L=608, C.I.=0.4984, R.I.=0.7366). *Camposaurus* was found to be a member of the coelophysid clade in all the trees, under the definition of the name I advocate above (="*Syntarsus*" *kayentakatae* + *Coelophysis bauri* and all descendents of their most recent common ancestor) (Fig. 112A). However, its position was uncertain within the coelophysid clade.

The taxon was found to be in a basal polytomy with the Shake-N-Bake taxon, a *Syntarsus rhodesiensis* + *Coelophysis* clade, and a "*Syntarsus*" *kayentakatae* + *Segisaurus* clade in both the majority rule and Adams consensus trees (Figs. 112B, C).

The remains attributed to *Camposaurus arizonensis* were recovered from the *Placerias* Quarry, a highly fossiliferous locality near St. Johns, Arizona. The stratigraphic level of the *Placerias* Quarry was traditionally recognized as being within the lower Petrified Forest Member of the Chinle Formation (Repenning et al., 1969; Jacobs and Murry, 1980; Long and Padian, 1986; Fiorillo and Padian, 1993; Long and Murry consensus, 1995; Fiorillo et al., 2000). Recent works that attempted to revise the Upper Triassic stratigraphic nomenclature of southwestern North America placed the *Placerias* Quarry within either the Blue Mesa Member of the Petrified Forest Formation of the Chinle Group (Hunt and Lucas, 1994), or within the Bluewater Creek Formation of the Chinle Group (Lucas et al., 1997; Lucas, 1998; Heckert and Lucas, 1998). Regardless of stratigraphic nomenclature, the works listed above generally agree that the fossil-bearing deposit was laid down in late Carnian time (Weishampel et al., 2004). This places *Camposaurus arizonensis* as the oldest unequivocal coelophysoid yet known, and extends the minimum divergence between Ceratosauria and Tetanurae into late to mid-Carnian time (Fig. 112D).

Gojirasaurus quayi is known from incomplete remains collected in the Cooper Canyon Formation (Dockum Group) of eastern New Mexico (Parrish and Carpenter, 1986; Carpenter, 1997). The taxon is most notable for the size of the immature individual represented by the fossil material. Measurements of the tibia, pubis, and

scapula indicate an individual more than five meters in reconstructed length, making *Gojirasaurus* one of the largest known Triassic theropods. When the taxon was added to phylogenetic test 3, the analysis yielded 8250 equally most parsimonious trees (L=609, C.I.=0.4975, R.I.=0.7362) (Figs. 113A-C). *Gojirasaurus* was unequivocally a coelophysoid in all the recovered trees, but its phylogenetic position beyond that level of resolution was uncertain (Fig. 113A). The taxon was placed in a polytomy with *Dilophosaurus* and more derived coelophysoids in the Adams cladogram (Fig. 113B), and more derived than *Dilophosaurus*, but in a basal polytomy with *Zupaysaurus*, *Liliensternus*, and Coelophysidae in the 50% majority-rule consensus cladogram (Fig. 113C). The incompleteness of the specimen (9.8% complete; Table 5) and lack of unambiguous, derived characters preserved in the material prevented more conclusive hypotheses of its position relative to other coelophysoids.

The unit that produced the remains of *Gojirasaurus quayi* was labeled the Bull Canyon Formation by Lucas and Hunt (1989), a convention also used by Long and Murry (1995). However, Lehman et al., (1992) and Lehman (1994a, 1994b) demonstrated that the "Bull Canyon Formation" of eastern New Mexico was laterally and lithologically equivalent to the revised Cooper Canyon Formation of western Texas, a conclusion agreed upon by Carpenter (1997). The Cooper Canyon Formation was interpreted to be of early to mid-Norian age (Chatterjee, 1986; Carpenter, 1997; Weishampel et al., 2004). If this is correct, the presence of *Gojirasaurus* in sediments of this age represents only a slight back-dating of the minimum divergence time between Coelophysidae and less

derived coelophysoids such as *Gojirasaurus*, *Zupaysaurus*, *Liliensternus*, and *Dilophosaurus* (Fig. 113D).

Procompsognathus triassicus, known only from a partial post-cranial skeleton from the Middle Stubensandstein of Germany, was previously allied to *Segisaurus halli* in some phylogenetic analyses (Sereno, 1997, 1998). *Procompsognathus* was used as a reference taxon by Sereno (1998) to anchor the clade name "Procompsognathinae" as the sister clade to "Coelophysinae". The addition of *Procompsognathus* to the matrix in phylogenetic test 3 resulted in 7450 equally most parsimonious trees (L=608, C.I.=0.4984, R.I.=0.7377). The strict cladogram of the 7450 trees showed a basal polytomy for all Coelophysoidea more derived than *Dilophosaurus*, including *Procompsognathus* (Fig. 114A). *Procompsognathus* was placed within Coelophysidae (under the taxonomy I advocate above) in both the Adams and 50% majority rule consensus cladograms (Figs. 114B, C). The coelophysid status of this early to middle Norian age taxon pushes back the minimum divergence time for the origin of Coelophysidae to this time (Fig. 114D).

Genusaurus sisteronus is represented by very incomplete remains from Albian age sediments of France (Acarrie et al., 1995). The addition of *Genusaurus* to phylogenetic test 3 resulted in 14,700 equally most parsimonious hypotheses of phylogeny (L=608, C.I.=0.4984, R.I.=0.7368). *Genusaurus* was found to be a ceratosauroid theropod, but its presence resulted in a basal polytomy of all the ceratosauroids other than a *Majungatholus* +*Aucasaurus* + *Carnotaurus* clade in the strict consensus tree (Fig. 115A). The Adams consensus cladogram placed *Genusaurus* in a

basal ceratosauroid polytomy with *Ceratosaurus*, *Elaphrosaurus*, and Abelisauria (Fig. 115B). *Genusaurus* was placed in a polytomy at the base of Abelisauria with Noasauridae and more derived abelisaurs in the 50% majority rule consensus tree (Fig. 115C). These phylogenetic results are generally consistent with the findings of Carrano et al. (2002). The status of *Genusaurus* as an Albian age ceratosauroid helps bridge a substantial temporal gap between the basal ceratosauroids *Elaphrosaurus* and *Ceratosaurus* (Late Jurassic), and the more derived abelisaurs known from the Late Cretaceous (Fig. 116D).

Shuvosaurus inexpectatus is represented by an incomplete skull and lower jaws from the Cooper Canyon Formation of western Texas (Chatterjee, 1993; Rauhut, 1997). It was originally described as a Late Triassic ornithomimoid (Chatterjee, 1993), but later cladistic analyses hypothesized *Shuvosaurus* was a basal theropod of uncertain affinities (Rauhut, 1997), or a member of the coelophysoid lineage (Rauhut, 2003). I re-interpreted a number of characters for the taxon, and added *Shuvosaurus* to phylogenetic test 3. The analysis resulted in 525 equally most parsimonious hypotheses of phylogeny (L=619, C.I.=0.4895, R.I.=0.7308). *Shuvosaurus* was placed as the most basal member of the theropod lineage in all 525 recovered trees (Figs. 116A-C). Its presence resulted in the removal of *Herrerasaurus* from the theropod lineage. *Herrerasaurus* was instead the most basal member of Saurischia in all trees that contained *Shuvosaurus*. The presence of *Shuvosaurus* in the analysis had no effect upon the relationships within Neotheropoda, and did not result in the removal of *Dilophosaurus* from the coelophysoid lineage as occurred in the analysis of Rauhut (2003) (Fig. 116B, C).

The phylogenetic position of *Shuvosaurus* as the most basal theropod does not push back any divergence times for any more derived clades of theropods (Fig. 116D). The presence of the more derived taxon *Eoraptor* in early Carnian age deposits anchors the minimum divergence time between the theropods and sauropodomorphs given the taxa used in my analysis. The skull and jaws of *Shuvosaurus* are highly derived and exhibit many unique features that make its phylogenetic position in any analysis suspect. If the taxon is a basal theropod, its presence in the early Norian age Cooper Canyon Formation implies at least two alternate scenarios of the divergence and early diversity of the theropod lineage. First, Theropoda (and hence Saurischia and Dinosauria) may have a longer history than previously thought, but that is yet undiscovered. Origins for Dinosauria and the basal divergences of the main dinosaurian lineages would have to have occurred early in at least Middle Triassic time in this scenario. Another possibility is that the fossil record as we now know it is reflective of the actual pattern of origin and diversification of basal Theropoda. Theropoda (as well as Saurischia and Dinosauria) originated late in Middle Triassic time, but diversified rapidly in Carnian time in this scenario. *Shuvosaurus* would represent a holdover from the initial diversification of theropods in this case, and could represent a lineage that was part of an early radiative experiment in theropod evolution.

Recently described ceratosauroids - Several new ceratosauroid taxa were announced, named, and described in a pair of recent papers, Wilson et al. (2003) and Sereno et al. (2004). I was made aware of these papers too late to evaluate the

accompanying taxon-character matrices in great detail or add the taxa to my primary phylogenetic analyses. Here I offer a brief discussion of these taxa and the tree topologies recovered from preliminary analyses that incorporated two of them.

Rajasaurus narmadensis was based upon a partial skeleton recovered from the Lameta Formation (late Maastrichtian) of western India (Wilson et al., 2003). The history of theropod taxonomy from Cretaceous sediments of India is long and complicated, with a number of the earliest erected taxa now recognized as being based upon unassociated, non-diagnostic, or lost specimens (Huene and Matley, 1933; Chatterjee 1978; Molnar et al., 1990; Chatterjee and Rudra, 1996; Wilson et al., 2003). The type specimen of *Rajasaurus* is from a site several hundred kilometers west of the Lameta Formation localities that produced the type and referred specimens of the putative abelisaurids *Indosuchus raptorius* and *Indosaurus matleyi* (Huene and Matley, 1933; Chatterjee, 1978; Chatterjee and Rudra, 1996). However, the braincase of *Rajasaurus* has features not present in the braincases of *Indosuchus* and *Indosaurus*, so it was probably justified to erect a new taxon for the new material from western India.

The type material of *Rajasaurus* exhibits several features normally associated with abelisaurid theropods. Some of the features include a dorsally projected parietal crest, supratemporal fenestrae that closely approach one another on the midline that pinch the parietals down to a narrow median crest posteriorly, cervical centra that retain flat or weakly concave anterior articular surfaces, and six centra incorporated into the sacrum. *Rajasaurus* also evidently had a median naso-frontal horn or other structure on the dorsal skull roof based upon the posterior end of the structure preserved along the anterior edge

of the frontals. A median horn on the frontal is present in *Majungatholus*, and the fused nasals in that taxon are also slightly enlarged to form a low, median structure (Sampson et al., 1998). *Rajasaurus* was included in phylogenetic analyses conducted by Wilson et al. (2003) and Sereno et al. (2004). Not surprisingly, the taxon was found to be a member of Abelisauridae, and more closely related to *Carnotaurus* than to *Abelisaurus* (Fig. 117). I did not conduct an analysis that included *Rajasaurus*, and I accept the phylogenetic results of Wilson et al. (2003) and Sereno et al. (2004) with regard to the phylogenetic affinities of the taxon.

At least four new ceratosauroid taxa were announced by Sereno et al. (2004), all from western Africa (Niger Republic) in deposits ranging from Early to early Late Cretaceous age. Two of the new taxa were named and described in some detail, and all the anatomical information provided here is taken from Sereno et al. (2004). *Spinostropheus gautieri* was based upon a partial but articulated vertebral column from the third cervical to the anterior sacrals, as well as the cervical and some less complete dorsal ribs. The cervical centra of *Spinostropheus* bear anterior and posterior pleurocoels as in ceratosaurs ancestrally. It appears from the description and illustrations that the pleurocoels are in the form of foramina leading to cavities within the centrum. The cervical vertebrae also bear epipophyseal-postzygopophyseal laminae, a feature shared by abelisauroids. The cervical epipophyses do not project dorsally above the neural spines, and the neural spines themselves are relatively tall and broad, unlike the condition in noasaurids and more derived adelisaurs. The cervical ribs are perforated by pneumatic foramina as in *Ceratosaurus*, *Majungatholus*, and some tetanurans (Sampson et al., 1998;

Madsen and Welles, 2000). The parapophyses of the dorsal vertebrae are projected laterally on distinct stalks, a feature also present in *Ceratosaurus*, *Carnotaurus*, and perhaps other ceratosauroids (Gilmore, 1920; Bonaparte et al., 1990; Britt, 1991). It is not clear from the description if the sacral neural spines and arches of *Spinostropheus* were fused, but ossified tendons were present along the lateral surface of the sacral neural spines. Ossified tendon bundles were also reported along the surface of the sacral neural spines of at least one specimen of *Ceratosaurus* (Britt et al., 2000).

The second taxon named by Sereno et al. (2004) was *Rugops primus*, represented by a single, mostly complete skull lacking the palatal bones and posterolateral parts of the skull roof. Many of the skull bones of *Rugops* bear sculpturing similar to that present in abelisaurids. The body of the premaxilla is anteroposteriorly short and dorsoventrally deep. The anterior process of the maxilla is short and deep, and the dorsal process of the maxilla is directly at a very high angle from horizontal. The maxillary antorbital foss is not laterally visible on the alveolar ramus of the maxilla, and is very narrow along the maxillary dorsal process. The parietals are pinched between the large supratemproal fenestra, forming a narrow saggital crest posteriorly. The parietals are also dorsally projected to form an enlarged transverse nuchal crest as in abelisaurids (Chatterjee, 1978; Bonaparte and Novas, 1985; Bonaparte et al., 1990; Sampson et al., 1998). The nasals are fused anteriorly, but not along their entire length. The lacrimal and prefrontal are only partially co-ossified versus completely fused in more derived abelisaurids (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Sampson et al., 1998), and a small gap encircled by the lacrimals, frontals, and postorbitals was probably present. The

dorsal roofing bones of the skull are not thickened unlike the condition in the more derived abelisaurids (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Sampson et al., 1998). *Rugops* bears no median horns or crests on the dorsal skull roof, and no supra-orbital horns rising from the frontals as variably present in abelisaurids (Bonaparte et al., 1990; Sampson et al., 1998; Coria et al., 2002; Wilson et al., 2003).

Spinostropheus gautieri and *Rugops primus* were added to the taxon-character matrix used in phylogenetic test 3 and coded from the limited information available from Sereno et al. (2004). The analysis was run with both of these new taxa added at the same time. The analysis recovered 4126 equally most parsimonious hypotheses of relationship (L=617, C.I.=0.4911, R.I.=7355). Both *Spinostropheus* and *Rugops* were placed along the abelisauroid lineage in all cases, but resolution was very poor in the strict consensus tree (Fig. 118A). Their presence also resulted in the placement of *Elaphrosaurus* as the most basal ceratosauroid in all the recovered trees (Fig. 118A). *Spinostropheus* was in a basal polytomy with *Xenotarsosaurus* and all more derived abelisauroids in the Adams consensus tree (Fig. 118B), and the most basal member of the abelisauroid lineage in the 50% majority rule consensus tree (Fig. 118C). The relatively basal abelisauroid position of *Xenotarsosaurus* was unusual in the Adams consensus cladogram of this analytical run. *Rugops* was placed in a basal polytomy with *Ilokelesia* and Abelisauridae in both the Adams and 50% majority rule consensus trees (Figs. 118B, C). The results were consistent with the phylogenetic positions of these two taxa recovered by Sereno et al. (2004).

The type specimen of *Spinostropheus* was collected from deposits approximately 135 million years in age (Sereno et al., 2004), placing it early in Early Cretaceous time (Neocomian: Hauterivian) (Fig. 118D). The taxon represents an important find because *Spinostropheus* is only 10 to 15 million years younger than *Elaphrosaurus* and *Ceratosaurus*, the most basal unequivocal members of the ceratosauroid lineage in my analysis. It is encouraging that the temporal distribution of *Spinostropheus* is generally consistent with its phylogenetic position as recovered by Sereno et al. (2004) and here.

The type specimen of *Rugops* was collected from deposits approximately 95 million years in age (Cenomanian), making it contemporaneous with *Ilokelesia* and *Xenotarsosaurus* (Fig. 118D). Again, the phylogenetic relationships recovered in the analysis of Sereno et al. (2004) and my analysis are consistent with the temporal distribution of the taxon. Sereno et al. (2004) identified *Rugops primus* as one of the earliest member of the Abelisauridae. This is only the case if the stem-based re-definition of the name Abelisauridae advocated by Wilson et al. (2003) is adopted. I do not accept the stem-definition of the name Abelisauridae sensu Wilson et al. (2003), but instead recognize the priority of the node-definition of the name erected by Sereno (1998) (Table 1). *Rugops* is not an abelisaurid sensu Sereno (1998), but rather is an abselisaur more closely related to *Carnotaurus* than to *Noasaurus*.

Two additional abelisauroids from Niger were briefly mentioned by Sereno et al. (2004), but they were not named. One taxon was identified as a noasaurid represented by a partial but articulated skeleton. The other was called an abelisaurid, and was represented by a pelvic girdle and a maxilla. Given the use of the stem-defined name

Abelisauridae by Sereno et al. (2004) it is possible that this second taxon is also an abelisaur outside of Abelisauridae (sensu Sereno, 1998) with closer affinities to *Carnotaurus* than to *Noasaurus*. Both specimens were collected from deposits reported to be approximately 110 million years in age (Sereno et al., 2004), pushing back the minimum divergence age between the two main abelisaur lineages back to at least earliest Albian time (Fig. 118D). Sereno et al. (2004) also claimed that *Deltadromeus agilis*, a Cenomanian age taxon first identified as a coelurosaurian tetanuran (Sereno et al., 1996), is actually a basal member of the Noasauridae. If this relationship is supported by additional analyses, *Deltadromeus* partially bridges the temporal gap between the Maastrichtian age noasaurids *Masiakasaurus* and *Noasaurus*, and the Albian age noasaurid from Niger (Fig. 118D).

***Herrerasaurus* and *Eoraptor* -** The hypothesized placement of *Eoraptor* as a more derived theropod than *Herrerasaurus* is likely to meet skepticism among some systematists working on basal theropods. The case was previously made that *Herrerasaurus* was a true theropod more derived than *Eoraptor* (Novas, 1993). Since then, a number of authors operated with this phylogenetic hypothesis as an untested assumption in outgroup selection, with accompanying effects upon character polarity and reconstructions of character evolution with Theropoda (Sereno et al., 1994; Sereno 1999; Currie and Carpenter, 2000; Carrano et al., 2002; Allain, 2002). It was recognized and acknowledged that a number of evolutionary reversals were required to place *Herrerasaurus* as a basal theropod more derived than *Eoraptor* (Novas, 1993; Rauhut,

2003). Other authors found different phylogenetic positions of *Herrerasaurus*, or at least reiterated the ongoing lack of consensus regarding its relationships to other theropods and saurischians (Gauthier, 1986; Holtz, 1998; Padian et al., 1999).

Herrerasaurus lacked several derived characters shared by basal sauropodomorphs, *Eoraptor*, and neotheropods. Some of these derived states included a broad external antorbital fenestra (sensu Witmer, 1997), a dorsoventrally tall lacrimal, a foramen in or along the anteroventral edge of the splenial, and a first metacarpal with asymmetrical distal condyles in which the lateral condyle projects more distally than the medial condyle. The incorporation of vertebra 28 into the sacral series (a caudosacral) may also be a derived feature not present in *Herrerasaurus*.

Eoraptor has been almost universally recognized as the most basal theropod since its preliminary description (Sereno et al., 1993). Early but limited phylogenetic analyses that determined its position, as well as the more recent and extensive results of Rauhut (2003) cited a handful of plesiomorphic characters in *Eoraptor* that seemed to verify its basal position even compared to *Herrerasaurus*. These included heterodont dentition with lanceolate premaxillary and anterior maxillary teeth with a basal constriction, rudimentary teeth on the palate, a short preacetabular process of the ilium ("brachyiliacic" sensu Colbert, 1964b), a lack of a distal pubic expansion or boot, first metacarpal longer than the first phalanx of digit I (I-1), and penultimate phalanx of digit III (III-3) shorter than each of the more proximal phalanges of digit III.

My analysis indicated *Eoraptor* shares a number of derived characters with Neotheropoda, to the exclusion of *Herrerasaurus*. Some of the synapomorphies included

an inverted "L" shaped lacrimal, incorporation of vertebra 25 to the sacral series (dorsosacral 1), a blade-like preacetabular process on the ilium, a postacetabular process of the ilium greater in length than the width of the acetabulum, a pubic fenestra (as defined above) in the puboischiadic plate, and a subrectangular distal tibia with a small posterolateral extension. It was reported that *Eoraptor* had three sacral vertebrae, which is also typical of basal sauropodomorphs and is one more than is present in *Herrerasaurus* (Sereno et al., 1993; Rauhut, 2003). As described above, it is equivocal whether vertebra 28 is also part of the sacral series in *Eoraptor*, which would result in a four-vertebra sacrum. The claim that *Eoraptor* has a "brachyiliacic" ilium is incorrect. The left ilium of the holotype specimen is badly eroded, which gives the impression the pre- and postacetabular processes are short and stout as in *Herrerasaurus* and basal sauropodomorphs. The right ilium is better preserved and bears a short, pointed, and blade-like preacetabular process, and the postacetabular process is longer than the diameter of the acetabulum.

An unexplored issue with regard to *Eoraptor* is the ontogenetic status of the known material. Several features suggest the type individual may be that of an immature individual. Many of the bones of the skull are not firmly sutured together. This is especially true of many of the braincase elements, including the frontals, parietals, supraoccipital, basisphenoid, and basioccipital. The proportions of the skull are reminiscent of other juvenile dinosaurs (Colbert, 1989; Varricchio, 1997), with an anteroposteriorly short, dorsoventrally deep rostrum and large orbit. It appears that the neural arches and vertebral centra are co-ossified through the anterior caudal vertebrae,

although it is difficult to discern the presence or absence of sutures between arches and centra in the cast available for study. The scapulae and coracoids show no signs of co-ossification. If the type of *Eoraptor* proves to be the remains of a juvenile individual, the taxon should be re-evaluated in cladistic analyses by leaving maturity-dependent characters scored as missing data for the taxon. Given the results of phylogenetic test 1 and the placement of the coelophysoid taxon *Liliensternus* (known only from immature specimens) in that test, there may be reason to suspect *Eoraptor* is in too basal a position on the theropod lineage.

Tests 1 and 2 tree topologies - Phylogenetic test 1 retained all the characters in the taxon-character matrix, and assumed that all the taxa within the analysis were represented by specimens that had reached the most advanced ontogenetic stage of their taxon's developmental pathways and morphology by the time of death. In other words, all taxa were treated as if they were represented by adult individuals. This set of parameters served as a proxy for the method of scoring characters employed by Carrano et al. (2002). Phylogenetic test 1 differed from the analysis of Carrano et al. (2002) in that the taxon-character matrix included characters first published by Rauhut (2003), as well as several novel characters.

I also coded a number of characters shared between my phylogenetic analysis and that of Carrano et al. (2002) differently. Reasons included different interpretations of anatomy, reassessment of previously known specimens, and data derived from new specimens. *Dilophosaurus* was the most heavily re-coded taxon shared between our

taxon-character matrices. Close scrutiny of the relatively mature *Dilophosaurus* specimen (UCMP 77270) provided unambiguous evidence for the presence of several maturity-dependent characters in the taxon that helped nest it securely within the coelophysoid lineage. These included co-ossification of the pelvic bones, co-ossification of sacral neural arch elements, co-ossification of sacral ribs and transverse processes to the ilia, development of a prominent trochanteric shelf on the proximal femur, and dimorphism in the proximal femur. These derived characters states were scored as unambiguously absent in previous analyses. This previously eliminated a number of synapomorphies shared by *Dilophosaurus* and other coelophysoids, and drew *Dilophosaurus* out of the coelophysoid clade. The revelation that *Dilophosaurus* possessed typical ceratosaur co-ossifications by late ontogeny had the effect of making *Liliensternus*, known only from relatively immature specimens, appear basal to the other ceratosaurs in test 1.

This illustrates the importance of accurate ontogeny estimation and treatment in phylogenetic analyses. Ontogenetic stage of the available fossil material cannot be ignored or it increases the likelihood of less-than-accurate hypotheses of phylogeny. *Liliensternus* was found to be a relatively derived coelophysoid in previous phylogenetic analyses, the sister taxon to Coelophysidae (Rowe, 1989; Rowe and Gauthier, 1990). Yet, in an analysis that assumed final ontogenetic stage in all taxa, and incorporated data from a relatively mature *Dilophosaurus* specimen, the position of *Liliensternus* was shifted to the most basal point on the ceratosaur lineage. I conclude that if the relative maturity of fossil material is ignored when characters are coded for a cladistic analysis,

there is increased potential that taxa known only from immature specimens will shift to relatively basal positions in the resulting hypotheses of phylogeny.

It was no surprise that phylogenetic test 2 resulted in hypotheses of phylogeny consistent with the results of Rauhut (2003). It is reasonable to assume that any time useful characters are removed from a phylogenetic analysis there is the potential that real data are being lost, and the likelihood of obtaining the true tree is decreased. The argument is whether characters that vary greatly through the ontogeny of an organism represent useful characters for phylogeny reconstruction. I argue that they are.

In his methodological explanation, Rauhut (2003:10) stated, "…fusion characters have been omitted completely. Fusion of elements often depends on the ontogenetic stage of the individual and might also be variable between individuals of the same age due to mechanical stress, pathologies, or size variation". The bony elements of the tetrapod skeleton undergo ossification after fertilization. The ossification of each bone in the skeleton occurs at a given point in ontogeny, as do the appearance and enhancement of processes, tubercles, muscle scars, and coalescence between ossification centers that eventually yield a single finished bone. Therefore, almost all skeletal data available to vertebrate paleontologists are a product of some event in the ontogeny of the individual organism. The reasons cited by Rauhut (2003) for exclusion of fusion characters in the skeleton can be applied to almost all osteological features.

The skeletal co-ossifications eliminated from consideration by Rauhut (2003) had the potential of being phylogenetically informative. Each co-ossification represented an event along the ontogenetic trajectory of an individual and assumedly the taxon to which

the individual belonged. The timing of an ontogenetic event along a given trajectory has the potential to be phylogenetically informative. The expression of a novel event or morphology along an ontogenetic trajectory has great potential to be phylogenetically significant. Treating fusion characters as uninformative represents a substantial loss of available phylogenetic data.

The ceratosaur skeleton is marked by a high degree of co-ossification (fusion in many cases) between many elements. These co-ossifications are not present in basal tetanuran taxa, but may be convergently present in derived coelurosaurian lineages. The a priori removal of co-ossification-based characters from a phylogenetic analysis almost guarantees that the resulting reconstructions of ceratosaur phylogeny will be less than accurate.

Rowe and Gauthier (1990) diagnosis - Ceratosauria (or more accurately, the most basal node of Ceratosauria) was diagnosed by ten synapomorphies by Rowe and Gauthier (1990). Subsequent authors debated the validity of these characters and their utility for diagnosing the clade (Cuny and Galton, 1993; Holtz, 1994; 1998; Carrano and Sampson, 1998; Forster, 1999; Carrano et al., 2002; Rauhut, 2003). It is now clear that not all of these characters diagnose Ceratosauria. Some diagnose less inclusive clades within Ceratosauria, while others have a more widespread distribution among theropods, or saurischians. The diagnostic characters of Rowe and Gauthier (1990) are listed and discussed below.

1). Two pairs of pleurocoels in the cervical vertebrae.

The presence of this condition was argued to be absent in a number of ceratosaurian theropods, including *Coelophysis* (Colbert, 1989), *Liliensternus* (Cuny and Galton, 1993; Rauhut, 2003), and *Masiakasaurus* (Carrano et al., 2002). The work of Britt (1993) concluded that two pleurocoels in each side of the cervical vertebrae was the plesiomorphic condition for Theropoda, and this study was cited by Rauhut (2003) as further support for the non-ceratosaurian nature of coelophysoids. In the hypothesis of Rauhut (2003), tetanurans possessed a derived condition of having lost the posterior pleurocoel in each cervical vertebra.

My analysis breaks up the evolution of the cervical pleurocoels into two separate characters, the presence of a pleurocoel in the anterior part of each cervical centrum, and the presence of a pleurocoel in the posterior part of each cervical centrum. An anterior pleurocoel in each cervical centrum is diagnostic of Neotheropoda, being shared by ceratosaurs (including Coelophysoidea) and tetanurans. The presence of a posterior pleurocoel in each cervical centrum is a feature unique to Ceratosauria among the basal theropods, although the character may also appear convergently in some derived coelurosaur taxa (Makovicky, 1995).

2). Transverse processes of dorsal vertebrae strongly backturned and triangular when viewed from above.

The criticism leveled against this character is in part the result of ambiguity in the original concept of the character. The two modified characters that derived from this single character are unambiguously diagnostic of Ceratosauria in my analysis. See character descriptions above for detailed discussion of the distribution of these characters.

3). Pubic plate perforated by a large, circular, pubic fenestra lying below the obturator foramen.

This character is preserved in only a few ceratosaur taxa (*Ceratosaurus*, *Coelophysis*, *Syntarsus*, and *Segisaurus*), a fact recognized by Rowe and Gauthier (1990). This character was included in the analysis of Rauhut (2003), but was scored as absent in *Ceratosaurus*, *Liliensternus*, and *Elaphrosaurus*, as well as all other non-coelophysoid theropods. My concept of the pubic fenestra is different from that of Rowe and Gauthier (1990), and Rauhut (2003) (see above). The pubic fenestra represents a stage in the opening-up of the puboischiadic plate. A partial reduction of the puboischiadic plate may be present in *Eoraptor* and is present in some ceratosaurs. The pubic fenestra and pelvic fenestra (sensu Hutchinson, 2001a) eventually met and coalesced during the evolutionary history of Theropoda, and completely opened the osseous floor of the pelvic canal. The presence of a pubic fenestra is therefore not diagnostic of Ceratosauria in my results, but instead is present at the node encompassing *Eoraptor* and Neotheropoda ancestrally.

4). Sacral transverse processes, sacral ribs, neural arches, and spines completely fused to each other and sacral ribs fused to the ilium in adults.

This character encompassed several potentially independent character states as originally conceived. As a result, its validity was sometimes questioned when specimens of taxa were recovered that possessed some, but not all of the co-ossifications listed (Cuny and Galton, 1993; Carrano et al., 2002). The character was not used in the analysis of Rauhut (2003) because it involved the fusion of several skeletal elements. At

least two of the independent characters derived from the original character description are unambiguously diagnostic of Ceratosauria in my analysis.

5). Pubis, ischium, and ilium fused together in adults.

This fusion-based character was another criticized and removed from consideration by Rauhut (2003). The lack of fusion between the pelvic elements in some ceratosaurian taxa was cited as further evidence that the distribution of this character was far more limited than had been determined by Rowe and Gauthier (1990), and was of limited utility. Two errors were committed by Rauhut (2003) with regard to this feature. First, it was assumed that all the specimens of taxa such as *Dilophosaurus*, *Gojirasaurus*, *Liliensternus*, *Elaphrosaurus*, and abelisaurids were mature individuals that had reached the final stages of pelvic ossification. This assumption is highly doubtful for *Liliensternus* and *Gojirasaurus*, and remains equivocal for *Elaphrosaurus*, given the results of my ontogenetic analysis. Second, evidence or reports of co-ossification between pelvic bones was either missed or ignored for *Dilophosaurus* (UCMP 77270), *Carnotaurus* (Bonaparte et al., 1990), and *Ceratosaurus*. Co-ossification of the pelvic bones by adulthood is a diagnostic character supporting ceratosaurian monophyly in my results.

6). Trochanteric self present on lessor trochanter of femur in robust individuals.

The validity of this character as a ceratosaurian synapomorphy was legitimately questioned by Rauhut (2003). Besides being present in some coelophysoids, *Ceratosaurus*, and *Xenotarsosaurus*, a pronounced trochanteric shelf on the proximal femur is present in some dinosauriforms (e.g., *Marasuchus*, *Silesaurus*), *Herrerasaurus*,

and the basal sauropodomorph *Saturnalia* (Gilmore, 1920; Raath, 1977, 1990; Martinez et al., 1986; Colbert, 1989, 1990; Rowe, 1989; Bonaparte et al., 1990; Novas, 1993; Sereno and Arcucci, 1994; Langer et al., 1999; Madsen and Welles, 2000; Dzik, 2003; Langer, 2003, 2004). It is likely the trochanteric shelf was plesiomorphic for Dinosauria. The structure was independently lost in Ornithischia, sauropodomorphs more derived than *Saturnalia*, tetanurans, some ceratosauroids, and gracile adults of at least some coelophysoid taxa. Its presence in the aforementioned ceratosaurs represents retention of a plesiomorphic feature, and is not diagnostic of Ceratosauria. Replacement of the pronounced trochanteric shelf by a low, mound-like trochanteric shelf is a valid phylogenetic character.

7). A sulcus excavated into the base of crista tibiofibularis.

This character is difficult to assess in some specimens and descriptions, so it is no surprise that its distribution among many taxa was sometimes questioned. The degree to which the sulcus is excavated into the lateral base of the crista tibiofibularis of the femur may depend in part upon the relative ontogenetic stage of the individual specimen, as well as the quality of preservation of the specimen. For example, the sulcus is clearly present in the type of *"Syntarsus" kayentakatae* (MNA V2623), but is not expressed in a sub-adult specimen of the same taxon (TMM 43688-1). My analysis shows this character is diagnostic of Ceratosauria. Criticism of this character by Rauhut (2003) was invalid because the structure was misidentified and confused with a different feature on the proximal end of the fibula.

8). Astragalus and calcaneum fused to each other and to the tibia in late ontogeny.

This character encompassed two independent variables, which caused difficulties when specimens were found that possessed one, but not both features. For example, the astragalus and calcaneum of at least one *Liliensternus* individual are fused, but the resulting astragalocalcaneum is not fused to the distal tibia (Huene, 1934). This is attributed to the relative immaturity of the individual specimen, but a chance remains that it is phylogenetically controlled. The adult specimen of *Dilophosaurus* (UCMP 77270) shows no sign of astragalus-tibia co-ossification, another sign that the two variables included in the original character description should be treated as separate evolutionary transformations. Fusion of the astragalus and calcaneum by adulthood is unambiguously diagnostic of Ceratosauria in my analysis. The apparent lack of co-ossification between the tibia and astragalus in *Dilophosaurus*, *Liliensternus*, and *Zupaysaurus* suggests this character evolved independently in a Shake-N-Bake taxon + more derived coelophysids clade and Neoceratosauria.

9). Ascending process of astragalus directed vertically, subparallel with tibial shaft, and largely overlapped rostrally by fibula.

It was correctly pointed out (Rauhut, 2003) that the first two components of this character represent plesiomorphic states of the ascending process of the astragalus among neotheropods. The anterior overlap of the ascending process by a flange of the distal fibula is not present in ornithischians, sauropodomorphs, *Herrerasaurus*, or tetanurans, but it is clearly present in specimens of *Coelophysis*, *Syntarsus rhodesiensis*, the Shake-N-Bake taxon, and *"Syntarsus" kayentakatae*. It is also present in *Ceratosaurus* (Gilmore, 1920; Madsen and Welles, 2000). Distribution of this character among

abelisaurids is unknown or not described. My analysis shows the fibular overlap of the ascending process to be diagnostic of the Shake-N-Bake taxon + Coelophysidae clade within Coelophysoidea, and independently evolved in *Ceratosaurus*.

10). Distal tarsals II and III fused to their respective metatarsals by late ontogeny.

There is no evidence for an ossified distal tarsal II in any coelophysoid, or any other theropod for which an adequate description of articulated distal tarsal elements is given. This being stated, it can be difficult to see distal tarsal III in specimens that underwent fusion between the distal tarsal and its metatarsal. The character is also dependent upon the ontogenetic status of the individual, so scoring the character as absent in taxa represented by immature material (e.g., *Liliensternus*, *Dilophosaurus*) is not warranted. Because of the uncertainty of the character in *Dilophosaurus*, *Liliensternus*, *Zupaysaurus*, and ceratosauroids, this feature is diagnostic of Coelophysoidea only under ACCTRAN character state optimization. It is diagnostic of a Shake-N-Bake taxon + more derived coelophysids clade under DELTRAN optimization.

The majority of characters cited by Rowe and Gauthier (1990) remain diagnostic of Ceratosauria, albeit some in altered form. Claims that these characters were of doubtful validity or utility in reconstructing basal theropod phylogeny were incorrect. Such claims were based upon incorrect assumptions, and in some cases inaccurate data. All but one (presence of a trochanteric shelf on the proximal femur) are diagnostic of clades within Ceratosauria.

Tykoski and Rowe (2004) diagnosis - An updated compilation of the state of understanding of Ceratosauria by Tykoski and Rowe (2004) was released recently, as part of the second edition of "The Dinosauria" (Weishampel et al., 2004). There was a long hiatus between manuscript submission and actual publication of the volume, with the result that a number of new discoveries and analyses pertinent to our understanding of Ceratosauria were published during the intervening time (Carrano et al., 2002; Arcucci and Coria, 2003; Rauhut, 2003). I also examined specimens of *Dilophosaurus wetherilli*, *Segisaurus halli*, and *Camposaurus arizonensis* at the University of California Museum of Paleontology subsequent to submission of the manuscript. A number of new and informative pieces of *Dilophosaurus*, *"Syntarsus" kayentakatae*, and the Shake-N-Bake taxon in the collections of the Texas Memorial Museum were prepared and studied over the same time. The end result was that the phylogenetic analysis conducted by Tykoski and Rowe (2004) was effectively obsolete by the time it was published. It is likely that the work will be in circulation for a long time before a third edition of "The Dinosauria" is attempted, so I address the diagnoses of Ceratosauria provided by Tykoski and Rowe (2004) here.

Ceratosauria was diagnosed on the basis of 13 unambiguous synapomorphies and another 12 ambiguously diagnostic characters by Tykoski and Rowe (2004). The unambiguous diagnostic characters included: 1) axial neural spine extends anteriorly beyond prezygapophyses; 2) post-axial neural spines dorsoventrally low; 3) dorsal transverse processes posteriorly backswept and triangular in dorsal view; 4) sacral ribs fuse with ilia; 5) brevis fossa of ilium distal (posterior) end broad; 6) supraacetabular

crest of ilium flares laterally and ventrally, overhanging much of anterodorsal half of acetabulum in lateral view; 7) pubic shaft axis bows anteriorly; 8) dimorphism in femoral anterior (=lessor) trochanter present; 9) femoral medial epicondyle well developed and crest-like; 10) distal femur's tibiofibular crest (=crista tibiofibularis, = ectocondylar tuber, =tuberous process) is sharply separated from fibular condyle; 11) astragalus and calcaneum fuse to form astragalocalcaneum in adults; 12) distal tarsal IV with large rectangular notch in posterolateral margin; 13) two pleurocoels in the post axial cervical and anterior dorsal vertebrae.

Seven of these characters remain diagnostic for Ceratosauria in my current analysis. They include characters 1, 3, 5, 8, 10, 11, and 13 (in modified form). Character 2 is diagnostic of Saurischia under ACCTRAN character state optimization, or of Abelisauria and a *Liliensternus* + more derived coelophysoids clade under DELTRAN character state optimization. Character 4 is diagnostic of Ceratosauria only under DELTRAN character state optimization. Character 6 is potentially diagnostic of Ceratosauria only under ACCTRAN character state optimization, and character 7 is potentially diagnostic of Ceratosauria only under DELTRAN character state optimization. Characters 9 and 12 are not diagnostic of Ceratosauria or any clade within it. The presence of two pairs of pleurocoels in the cervical vertebrae (character 13 above) is diagnostic of Ceratosauria. It was unclear to Tykoski and Rowe (2004) whether this condition arose from an ancestor with one pleurocoel already present or an ancestor that lacked cervical pleurocoels. Treating anterior and posterior pleurocoels as separate characters in my analysis (per Carrano et al. [2002]) provided the answer to the

uncertainty. An anterior pair of pleurocoels in each cervical vertebra arose in Neotheropoda, and the development of a posterior pair of pleurocoels in each cervical centrum is unique to ceratosaurs among basal Theropoda.

Several of the characters listed as only ambiguously diagnostic of Ceratosauria by Tykoski and Rowe (2004) are synapomorphies of the clade in my analysis. These include an anterodorsally convex, blade-like axial neural spine; very thin, elongate cervical ribs; sacral centra fused to extreme degree; sacral neural arch elements (transverse processes, arches, neural spines) and sacral ribs fused to one another; and ilium dorsal margin relatively linear.

Directions of future work - The greatest obstacle to obtaining better reconstructions of basal theropod phylogeny is a lack of accurate and thorough anatomical descriptions for a number of important taxa. The most glaring example of this is *Coelophysis bauri*. *Coelophysis* is the best represented Triassic theropod, with dozens of skeletons and many hundreds of less complete pieces deposited in collections around North America. Despite this, almost all of our knowledge of the anatomy of this important taxon comes from only one or two published works that unfortunately contain many inaccuracies (Colbert, 1989, 1990). *Coelophysis* is also somewhat contradictory in that it is an early coelophysoid in temporal terms (late Norian), yet is also one of the most derived taxa in the clade. This suggests either there is a long evolutionary history of coelophysoids yet unrepresented by the fossil record, or the lack of accurate anatomical information about the taxon skewed my phylogenetic results.

Coelophysis also presents the best opportunity to obtain further ontogenetic data for Coelophysoidea, and test the accuracy of the quantitative ontogenetic assessment method I use here. The large number of specimens and the range of individual sizes offer an excellent chance to map the distribution of many ontogenetic characters that cannot be confidently coded in other coelophysoid taxa. Some of these include the sequence of neurocentral suture closure for the entire vertebral column, patterns of sacral centrum incorporation though ontogeny, and the sequence of co-ossification between the pelvic bones. There are probably enough specimens of *Coelophysis* known to test and map the ontogeny of this single taxon alone, which would then provide a baseline against which the ontogenetic pathways of other coelophysoids could be assessed.

Another area that warrants future investigations is continued exploration of the Glen Canyon Group and related units of the southwestern United States. The Kayenta Formation is by far the most productive vertebrate fossil bearing unit of the Glen Canyon Group, although important finds are also known from the underlying Moenave Formation and the overlying Navajo Sandstone. The Kayenta Formation has produced among the most diverse assemblage of theropods known from Late Triassic to Early Jurassic age sediments in the world, with a minimum of three distinct coelophysoid taxa (*Dilophosaurus wetherilli*, "*Syntarsus*" *kayentakatae*, and the Shake-N-Bake taxon) from this one geologic formation. The recent discoveries of new theropod specimens from the Kayenta Formation contributed greatly to my work. Future preparation of additional material will continue to provide new and important data that will improve understanding of the anatomy and phylogeny of coelophysoid theropods.

The Navajo Sandstone is the upper unit of the Glen Canyon Group, and is generally viewed as being late Early Jurassic in age (Pliensbachian-Toarcian). This is tantalizingly close in age to one of the great gaps in the theropod fossil record. There is an unfortunate lack of vertebrate fossil bearing terrestrial sediments from Middle Jurassic time in North America. The situation is not much better on other continents. It appears that tetanuran theropods began their great diversification by the Middle Jurassic, as indicated by remains of basal tetanurans from Europe and Asia.

The Navajo Sandstone has produced only a few incomplete vertebrate body fossils, including specimens of prosauropods, the partial skeleton of *Segisaurus halli*, and fragmentary remains of a small protosuchid crocodyliform (Camp, 1936; Galton, 1976; Clark and Fastovsky, 1986). The lack of vertebrate remains may be a result of low level of vertebrate habitation in the erg now represented by the Navajo Sandstone. Another possibility may be the rather limited exploration of the unit by vertebrate paleontologists. Most of the body fossils cited above come from the same general vicinity near Shonto, Arizona, in the Segi Canyon area (Clark and Fastovsky, 1986). The Navajo sandstone is a cliff-forming unit across much of its exposure, and is difficult to traverse. The Navajo Sandstone is thinner in the vicinity of the Adeii Eechii Cliffs than in the classic outcrops of the unit in southern Utah and Colorado. It also weathers into lower, rounded outcrops and ledges that form the highest rim of the Adeii Eechii Cliffs.

The scarcity of North American terrestrial vertebrate fossils of late Early and Middle Jurassic age makes the prospect of further investigations in the Navajo Sandstone intriguing. Any new material found from this unit would represent a contribution to our

understanding of vertebrate diversity in the region at the time. The odds are also good that new taxa or new specimens of known Navajo Sandstone taxa (e.g., *Segisaurus*) would add new data to phylogenetic studies of basal theropod evolution. The act of prospecting in the exposures of the Navajo Sandstone can be physically demanding, but the potential reward for finding new vertebrate material in the upper most formation of the Glen Canyon Group is substantial.

CONCLUSIONS

The tests conducted in this work establish the following points. First, it sustains earlier work (Brochu, 1992, 1996; Colbert, 1999) establishing that parsimony based algorithms can be used as an effective tool to establish the degree of relative maturity expressed in fossil remains. Instead of ad hoc estimates of the ontogenetic stage preserved in fossil organisms based upon only a single or few ontogenetically variable features, such as neural arch-centrum co-ossification, a greater array of these characters can be subjected to analysis. The resulting hypothesis (or hypotheses) of relative degree of maturity, depicted graphically as an ontogram, provide more testable and data-supported criteria for assigning individual specimens to particular stages of development (i.e., juvenile, sub-adult, or adult). This technique can be applied to multiple individuals of a single taxon, or in the case of my analysis, to multiple individuals of closely related taxa. The technique should be restricted to taxa that are closely related and share a high degree of similarity in form when multiple taxa are evaluated in the analysis. This increases the likelihood that the taxa shared a similar ontogenetic trajectory.

An ontogenetic analysis was conducted on several specimens of multiple coelophysoid theropod taxa. The analysis generated useful hypotheses of relative maturity among the coelophysoid specimens, as well as hypotheses of the sequence of ontogenetic transformations that occured through the development of coelophysoid theropods. The latter finding should provide a useful guide to future researchers when trying to assess the ontogenetic stage preserved in the anatomy of coelophysoid fossils. No specimens of *Coelophysis bauri* were used in the ontogenetic analysis, but the taxon

has the potential to be the best-sampled and most informative taxon for establishing the relative sequence of coelophysoid ontogeny. There is a good chance that adding *Coelophysis* specimens to an ontogenetic analysis or conducting a single-taxon ontogenetic analysis of the taxon will result in a reappraisal and revision of the relative ontogenetic sequence of coelophysoid theropods.

The results of the analysis revealed that some taxa that had been used in phylogenetic analyses of basal theropod relationships were not known from any adult individuals (Figs. 5, 6). Little attempt was made in earlier analyses to address the effect the relative immaturity of the material representing these taxa had upon the phylogenetic hypotheses generated by the studies. Taxa known only from immature individuals included *Liliensternus liliensterni* and *Segisaurus halli*. It was found that most of the known *Dilophosaurus wetherilli* specimens were remains of juvenile individuals. These included the type (UCMP 37302) and referred specimens (UCMP 37303, TMM 43646) of *Dilophosaurus*. A single *Dilophosaurus* specimen (UCMP 77270) was the only adult known for the taxon. Most of the previous phylogenetic analyses that included *Dilophosaurus* did not fully recognize many of the features present in the adult *Dilophosaurus* specimen. The taxon was coded for a large number of maturity-dependent characters in these earlier analyses, based upon the morphologies expressed in the better known and fully described immature specimens.

An extensive parsimony-based analysis of basal theropod phylogeny was conducted to determine the position of Coelophysoidea relative to other theropods. Characters were re-evaluated for many coelophysoid taxa based upon my interpretations

of morphology and character descriptions, and new data from recently collected specimens were applied to character coding. The analysis was run three times, each adopting a different approach to the recognition and treatment of the ontogenetic status of the material representing some coelophysoid taxa. The intent was to approximate the methods used in addressing ontogenetic factors in previous analyses of basal theropod phylogeny. The first test coded all the characters in the analysis as if the known specimens of each taxon preserved the full adult stages of ontogenetic development. The second test deleted characters from the analysis that were judged to be too dependent upon ontogeny or varied too unpredictably with regard to ontogeny. The third test incorporated the results of my ontogenetic analysis. Those taxa that were found to be known only from immature individuals (*Liliensternus*, *Segisaurus*) or had been coded previously based upon immature specimens (*Dilophosaurus*) were reassessed with regard to the ontogenetically variable and dependent characters in the analysis. Characters states that were found to be expressed only in later stages of ontogeny (i.e. adulthood) were coded as missing data if specimens of the pertinent taxa were too immature for the character to have been expressed by the time of death.

The first test (the 'all-adults' approach)generated hypotheses of phylogeny found Coelophysoidea was nested within Ceratosauria (Fig. 106). *Liliensternus liliensterni* was placed as the most basal member of the ceratosaurian lineage, a result inconsistent with previous analyses. The ontogenetic analysis demonstrated that no adult specimens of *Liliensternus* were known. I predict that immature fossil taxa (=those not represented by specimens of mature individuals) may be placed in basal positions in cladistic analyses

that also include mature taxa (=taxa known from mature individuals), but that fail to code characters to reflect the relative maturity expressed in the fossils.

The second phylogenetic tests (the 'character-deletion' approach) generated hypotheses of phylogeny consistent with recent works that found Coelophysoidea was placed outside the Ceratosauria + Tetanurae clade (Carrano et al., 2002; Rauhut, 2003; Wilson et al., 2003) (Fig. 107). *Dilophosaurus* was nested within Coelophysoidea under both of these phylogenetic tests, contrary to the findings of Carrano et al. (2002) and Rauhut (2003). I attribute this to different interpretations of the anatomy of this and other coelophysoid taxa, data from new specimens not available to earlier authors (TMM 43646), and data derived from the only adult specimen of *Dilophosaurus* known (UCMP 77270).

The third phylogenetic test coded maturity-dependent characters in certain taxa to reflect the relative maturity exhibited by representative specimens of those taxa. It generated hypotheses of basal theropod phylogeny that placed Coelophysoidea as the sister lineage to Ceratosauroidea within Ceratosauria, the 'traditional' arrangement of the two lineages (Fig. 108) (sensu Gauthier, 1986; Rowe, 1989; Rowe and Gauthier, 1990; Holtz, 1994, 1998; Sereno, 1999a). *Dilophosaurus* was the most basal coelophysoid in these hypotheses. *Zupaysaurus rougieri* was a member of the coelophysoid lineage, and not a tetanuran theropod as originally suggested (Coria and Arcucci, 2003). *"Syntarsus" kayentakatae* and *Syntarsus rhodesiensis* were not sister-taxa in the hypotheses generated by this test (or either of the others). *Syntarsus rhodesiensis* and *Coelophysis* were sister taxa in these hypotheses. The Shake-N-Bake taxon was labile within the *Coelophysis* +

Syntarsus rhodesiensis + *Segisaurus* + *"Syntarsus" kayentakatae* clade, variously adopting sister-taxon relationships with all of these taxa in the hypotheses. This can probably be attributed to the fragmentary and incomplete nature of the Shake-N-Bake material and the limited number of characters that could be coded for the taxon.

Elaphrosaurus bambergi and *Ceratosaurus nasicornis* vied for the most basal position of the ceratosauroid lineage (Fig. 108A). It required only two additional evolutionary steps to place *Elaphrosaurus* within the coelophysoid lineage. The single known specimen of *Elaphrosaurus* lacks cranial material, and the possibility should be kept open that future discoveries could yet swing the taxon over onto the coelophysoid lineage. There were no exceptionally unexpected relationships within the rest of the ceratosauroid lineage as compared to the results of Carrano et al. (2002), and Rauhut (2003).

The ontogenetic stage of individuals of extinct fossil taxa can and should be assessed using parsimony-based algorithms. Ontogenetic transformations can be mapped along a relative ontogenetic hierarchy of individual specimens. The resulting sequence of transformations can be used to identify in which stage of life development an individual fossil organism died. This information should then be applied to any phylogenetic analysis that uses maturity-dependent characters. The derived character states of maturity-dependent characters that have no potential for being expressed in certain fossil taxa, because the known specimens of the taxa are too immature to express them, should be coded as missing data, and not as absent in the taxa. This approach is superior to simply ignoring the ontogenetic status of known specimens, and to a priori deletion of

maturity-dependent characters. The results of a phylogenetic study that incorporates the findings of a quantitative ontogenetic analysis in character coding should yield a more robust and testable hypothesis of phylogeny.

TABLE 1. Taxonomic definitions. Status of names as either node- or stem-based definitions indicated. Reference taxa for node-based names presented in format of, "Taxon A and Taxon B", indicating clade encompasses most recent common ancestor of Taxon A and Taxon B and all of its descendants. Reference taxa for stem-based names presented in format of, "Taxon A than Taxon B", indicating lineage includes Taxon A and all taxa more closely related to Taxon A than to Taxon B. Original use of name is given under "Taxon Name". First taxon-based phylogenetic definition for the name is given under "Phylogenetic Definition".

			Reference Taxa		
Taxon Name	**Phylogenetic Definition**		**A**		**B**
Abelisauria Novas, 1992	Novas, 1997	node	*Noasaurus*	and	*Carnotaurus*
Abelisauridae Bonaparte and Novas, 1985	Sereno, 1998	node	*Abelisaurus*	and	*Carnotaurus*
Abelisauroidea Bonaparte, 1991	Holtz, 1994	stem	*Carnotaurus*	than	*Ceratosaurus*
Archosauria Cope, 1869	Gauthier, 1986	node	Crocodylia	and	Aves
Aves Linneus, 1758	Gauthier, 1986	node	Neognathae	and	Paleognathae
Avetheropoda Paul, 1988	Padian et al., 1999	node	*Allosaurus*	and	Aves
Ceratosauria Marsh, 1884	Rowe, 1989	stem	*Ceratosaurus*	than	Aves
Ceratosauroidea Bonaparte, 1991	Sereno, 1998	stem	*Carnotaurus*	than	*Coelophysis*
Coelophysidae (Nopsca, 1928)	Holtz, 1994	node	*Coelophysis*	and	*Syntarsus*
Coelophysoidea Holtz, 1994	Sereno, 1998	stem	*Coelophysis*	than	*Ceratosaurus*
Coelurosauria Huene, 1914	Gauthier, 1986	stem	Aves	than	*Allosaurus*
Dinosauria Owen, 1842	Padian and May, 1993	node	*Triceratops*	and	Aves
Dinosauriformes Novas, 1992	Novas, 1996	node	*Marasuchus*	and	Aves
Neoceratosauria Novas, 1992	Holtz, 1994	node	*Ceratosaurus*	and	*Carnotaurus*
Neotheropoda Bakker, 1986	Holtz, 1998	node	*Ceratosaurus*	and	Aves
Noasauridae Bonaparte and Powell, 1985	Wilson et al. 2003	stem	*Noasaurus*	than	*Carnotaurus*
Ornithischia Seeley, 1888	Padian and May, 1993	stem	*Triceratops*	than	Aves
Saurischia Seeley, 1888	Gauthier, 1986	stem	Aves	than	*Triceratops*
Sauropodomorpha Huene, 1932	Gauthier, 1986	stem	*Plateosaurus*	than	Aves
Tetanurae Gauthier, 1986	Gauthier, 1986	stem	Aves	than	*Ceratosaurus*
Theropoda Marsh, 1881	Gauthier, 1986	stem	Aves	than	*Cetiosaurus*

TABLE 2. Coelophysoid theropod specimens used in the ontogenetic analysis. Grouped by taxon.

Dilophosaurus wetherilli
- UCMP 37302
- UCMP 37303
- UCMP 77270
- TMM 43646 (a single individual with elements catalogued with separate specimen numbers-see Table 4)

Liliensternus liliensterni
- MB.R.2175 large
- MB.R.2175 small

Segisaurus halli
- UCMP 32101

Shake-N-Bake taxon
- MCZ 9442
- MCZ 9463
- TMM 43689-4

"Syntarsus" kayentakatae
- MNA V2623
- TMM 43669-3
- TMM 43688-1

Syntarsus rhodesiensis
- QG1

TABLE 3. Ontogenetic transformations in coelophysoid theropods. Sequence lists ontogenetic character transformations as distributed on the ontogram in Figure 6. Sequence listed as lower case Roman numerals, with "i" occurring in the early stages of ontogeny. Ambiguous character state transformations written in reduced type size. (A) indicates position of character transformation under ACCTRAN optimization. (D) indicates position of character transformation under DELTRAN optimization. V# = vertebra number counting posteriorly from skull.

i. 32. Ischia distal tips co-ossified
39. Sharp sulcus or concavity separates tibiofibular crest and fibular condyle of femur
(A) 2. Exoccipitals and basioccipital suture in occipital condyle

ii. 3. Supraoccipital, exoccipitals, and parietals suture
6. Dorsosacral 1 (V25) neural arch and centrum suture
9. V28 neural arch and centrum fuse
15. Sacral 1 (V26) centrum and ribs suture
16. Sacral 2 (V27) centrum and ribs suture
25. Anterior caudal neural arches suture to centra
(A) 14. Dorsosacral 1 (V25) centrum and ribs suture
(A) 17. Sacral (V25-28) neural arches and spines fuse
(A) 18. Sacral (V25-28) transverse processes coalesce to form horizontal lamina
(D) 2. Exoccipitals and basioccipital suture in occipital condyle

iii. 7. V26 neural arch and centrum suture
13. Sacral 2 (V27) and caudosacral 1 (V28) centra suture
(A) 1. Basisphenoid and basioccipital fuse
(A) 2. Exoccipitals and basioccipital fuse in occipital condyle
(A) 3. Supraoccipital, exoccipitals, and parietals fuse
(A) 6. V25 neural arch and centrum fuse
(A) 8. V27 neural arch and centrum fuse
(A) 9. V28 neural arch and centrum fuse
(A) 11. Dorsosacral 1 (V25) and sacral 1 (V26) centra fuse
(A) 12. Sacral 1 (V26) and sacral 2 (V27) centra suture
(A) 19. Dorsosacral 1 - caudosacral 1 (V25-28) transverse processes fuse to ilia
(A) 20. Dorsosacral 2 (V24) transverse processes fuse to ilia
(A) 26. Scapula and coracoid suture
(A) 27. Scapula-coracoid anterior margin contact continuous (no notch)
(A) 33. Femur proximal end bone texture smooth and well-ossified
(A) 34. Femoral head smoothly contoured and well-developed
(A) 40. Femoral distal condyles smooth, rounded, finished surfaces
(A) 44. Astragalus and calcaneum suture

iv. (A) 5. V24 neural arch and centrum fuse
(A) 10. Dorsosacral 2 (V24) and dorsosacral 1 (V25) centra suture
(A) 12. Sacral 1 (V26) and sacral 2 (V27) centra fuse
(A) 13. Sacral 2 (V27) and caudosacral 1 (V28) centra fuse
(A) 14. Dorsosacral 1 (V25) centrum and ribs fuse

(A) 15. Sacral 1 (V26) centrum and ribs fuse
(A) 16. Sacral 2 (V27) centrum and ribs fuse
(A) 30. Pubis and ischium suture

v Sub-adult

43. Suture between astragalus and ascending process of astragalus fully closed
44. Astragalus and calcaneum fuse except on proximal surface where suture still visible

(D) 26. Scapula and coracoid suture

vi. 28. Ilium and pubis suture
29. Ilium and ischium suture
35. Femur develops pronounced trochanteric shelf (robust individuals)
36. Anterior trochanter of femur becomes pyramidal or spike-like (robust individuals)
41. Proximal fibula develops oblique ridge on medial surface

(A) 38. Infrapopliteal crest forms on distal femur
(A) 42. Distal fibula anteromedial flange overlaps ascending process of astragalus
(A) 44. Astragalus and calcaneum fusion complete
(A) 46. Distal tarsal III and metatarsal III suture
(A) 47. Metatarsals II and III proximal ends suture
(D) 10. Dorsosacral 2 (V24) and dorsosacral 1 (V25) centra suture
(D) 13. Sacral 2 (V27) and caudosacral 1 (V28) centra fuse
(D) 27. Scapula-coracoid anterior margin contact continuous (no notch)
(D) 30. Pubis and ischium suture

vii. 30. Pubis and ischium fuse

(A) 10. Dorsosacral 2 (V24) and dorsosacral 1 (V25) centra fuse
(A) 26. Scapula and coracoid fuse
(D) 5. V24 neural arch and centrum fuse
(D) 6. V25 neural arch and centrum fuse
(D) 7. V26 neural arch and centrum fuse
(D) 8. V27 neural arch and centrum fuse
(D) 9. V28 neural arch and centrum fuse
(D) 11. Dorsosacral 1 (V25) and sacral 1 (V26) centra fuse
(D) 12. Sacral 1 (V26) and sacral 2 (V27) centra fuse
(D) 14. Dorsosacral 1 (V25) centrum and ribs fuse
(D) 15. Sacral 1 (V26) centrum and ribs fuse
(D) 16. Sacral 2 (V27) centrum and ribs fuse
(D) 33. Femur proximal end bone texture smooth and well-ossified
(D) 34. Femoral head smoothly contoured and well-developed
(D) 38. Infrapopliteal crest forms on distal femur
(D) 40. Femoral distal condyles smooth, rounded, finished surfaces
(D) 46. Distal tarsal III and metatarsal III suture

viii Adult

21. Dorsosacral 1 (V25) ribs suture to ilia
22. Sacral 1 (V26) ribs fuse to ilia

37. Femoral medial epicondyle becomes a well-developed crest
(A) 23. Sacral 2 (V27) ribs fuse to ilia
(A) 29. Ilium and ischium fuse
(A) 46. Distal tarsal III and metatarsal III fuse
(A) 47. Metatarsal II and III proximal ends fuse
(D) 1. Basisphenoid and basioccipital fuse
(D) 2. Exoccipitals and basioccipital fuse in occipital condyle
(D) 3. Supraoccipital, exoccipitals, and parietals fuse
(D) 17. Sacral (V25-28) neural arches and spines fuse
(D) 18. Sacral (V25-28) transverse processes fuse to form horizontal lamina
(D) 19. Dorsosacral 1 - caudosacral 1 (V25-28) transverse processes fuse to ilia
(D) 20. Dorsosacral 2 (V24) transverse processes suture to ilia
(D) 26. Scapula and coracoid fuse

ix. 4. Cervical ribs fuse to vertebral parapophyses and diapophyses
24. Sacral ribs (dorsosacral 1 - sacral 2:V25-27) fuse to each other at distal ends
28. Ilium and pubis fuse
45. Astragalus and tibia fuse
(D) 23. Sacral 2 (V27) ribs fuse to ilia
(D) 29. Ilium and ischium fuse
(D) 42. Distal fibula anteromedial flange overlaps ascending process of astragalus
(D) 46. Distal tarssal III fuses to metatarsal III
(D) 47. Metatarsal II and III proximal ends fuse

x. (A) 10. Dorsosacral 2 (V24) and dorsosacral 1 (V25) centra sutured, not fused - R
(A) 20. Dorsosacral 2 (V24) transverse processes sutured, not fused to ilia - R
(A) 31. Pubis with distal expansion
(D) 45. Astragalus and tibia fuse

xi. None

xii. (A) 21. Dorsosacral 1 (V25) ribs fuse to ilia

TABLE 4. Operational Taxonomic Units used in phylogenetic analysis. Published works from which taxa were scored are given. Specimens personally examined for this study are listed for each applicable taxon.

Abelisaurus comahuensis - Bonaparte and Novas (1985)
Allosaurus fragilis - Gilmore (1920), Madsen (1976)
Aucasaurus garridoi - Coria et al. (2002)
Baryonyx walkeri - Charig and Milner (1997)
Camposaurus arizonensis - UCMP 34498 (holotype), referred specimens UCMP 25791, UCMP 138591, UCMP 139622
Carnotaurus sastrei - Bonaparte et al. (1990)
Ceratosaurus nasicornis - Gilmore (1920), Britt et al. (1999), Britt et al. (2000), Madsen and Welles (2000); MWC 1.1.1, braincase only
Coelophysis bauri - Colbert (1989, 1990); MCZ 4329, MCZ 4330, TMM 45559-1, TMM 45559-2, TMM 45559-3, TMM 45559-4, TMM 45559-5, TMM 45559-6, TMM 45559-7, TMM 45559-8, TMM 45559-9, TMM 45559-10, TMM 45559-11, TMM 45559-12, TMM 45559-13, TMM 45559-14, TMM 45559-15, TMM 45559-16, TMM 45559-17, TMM 45559-18, TMM 45559-19, TMM 45559-20, TMM 45559-21, TMM 45559-22
Dilophosaurus wetherilli - Welles (1984); TMM 41394-1, TMM 43646-2, TMM 43646-3, TMM 43646-15, TMM 43646-17, TMM 43646-26, TMM 43646-33, TMM 43646-36, TMM 43646-59, TMM 43646-60, TMM 43646-61, TMM 43646-62, TMM 43646-63, TMM 43646-64, TMM 43646-65, TMM 43646-66, TMM 43646-67, TMM 43646-68, TMM 43646-69, TMM 43646-70, TMM 43646-71, TMM 43646-72, TMM 43646-73, TMM 43646-74, TMM 43646-78, TMM 43646-79, TMM 43646-80, TMM 43646-140, TMM 43646-141, TMM 43646-142, TMM 43646-143, TMM 43662-2, TMM 43690-1, UCMP 37302 (holotype), UCMP 37303, UCMP 77270
Elaphrosaurus bambergi - Janensch (1925, 1929)
Eoraptor lunensis - Sereno et al. (1993); PVSJ 512 (holotype - skull only), TMM 43451-2 (cast of holotype skeleton PVSJ 512)
Eustreptospondylus oxoniensis - Huene (1926), Rauhut (2003)
Genusaurus sisteronis - Accarie et al. (1995), Carrano et al. (2002)
Gojirasaurus quayi - Parrish and Carpenter (1986), Carpenter (1997)
Herrerasaurus ischigualastensis - Novas (1993), Sereno (1993), Sereno and Novas (1993); PVSJ 407, TMM 43451-1 (cast of skull PVSJ 407)
Ilokelesia aguadagrandensis - Coria and Salgado (1998)
Irritator challengeri - Sues et al. (2002)
Lesothosaurus diagnosticus - Thulborn (1970, 1972), Santa Luca (1984), Sereno (1991)
Liliensternus liliensterni - Huene (1934)
Majungatholus atopus - Sampson et al. (1998)
Marasuchus lilloensis - Sereno and Arcucci (1994)
Masiakasaurus knopfleri - Carrano et al. (2002)

Noasaurus leali - Bonaparte and Powell (1980), Bonaparte (1991)
Ornitholestes hermanni - Osborn (1903, 1916)
Plateosaurus longiceps - Galton (1984b, 1990, 2001a), Galton and Upchurch (2004)
"Poekilopleuron" valedunensis - Allain (2002)
Procompsognathus triassicus - Ostrom (1981), Sereno and Wild (1992)
Rugops primus - Sereno et al. (2004)
Sarcosaurus woodi - Andrews (1921), Carrano and Sampson (2004)
Scutellosaurus lawleri - Colbert (1981); TMM 43663-1, TMM 43664-1, TMM 43669-5, TMM 43687-9, TMM 43687-16, TMM 43687-17, TMM 43687-20
Segisaurus halli - Camp (1936); UCMP 32101 (holotype)
Shake-N-Bake taxon - Tykoski (1998); MCZ 8817, MCZ 9442, MCZ 9443, MCZ 9444, MCZ 9445, MCZ 9446, MCZ 9447, MCZ 9448, MCZ 9449, MCZ 9450, MCZ 9451, MCZ 9452, MCZ 9453, MCZ 9454, MCZ 9455, MCZ 9456, MCZ 9457, MCZ 9458, MCZ 9459, MCZ 9460, MCZ 9461, MCZ 9462, MCZ 9463, MCZ 9464, MCZ 9465, MCZ 9466, MCZ 9467, MCZ 9468, MCZ 9469, TMM 43689-1, TMM 43689-2, TMM 43689-3, TMM 43689-4, TMM 43689-5, TMM 43689-6, TMM 43689-7, TMM 43689-8, TMM 43689-9, TMM 43689-10, TMM 43689-11, TMM 43689-12, TMM 43689-13, TMM 43689-14, TMM 43689-15, TMM 43689-16, TMM 43689-17, TMM 43689-18, TMM 43689-19, TMM 43689-20, TMM 43689-21, TMM 43689-22, TMM 43689-23, TMM 43689-24, TMM 43689-25, TMM 43689-26, TMM 43689-27, TMM 43689-28, TMM 43689-29, TMM 43689-30
Shuvosaurus inexpectatus - Chatterjee (1993), Rauhut (1997, 2003)
Spinostropheus gautieri - Sereno et al. (2004)
Suchomimus tenerensis - Sereno et al. (1998)
"Syntarsus" kayentakatae - Rowe (1989), Tykoski (1998); MNA V2623 (holotype), TMM 43648-9, TMM 43669-3, TMM 43688-1, UCMP 128659
Syntarsus rhodesiensis - Raath (1969, 1977, 1985, 1990)
Torvosaurus tanneri - Britt (1991)
Xenotarsosaurus bonapartei - Martinez et al. (1986); TMM 45591-1, cast of femur either UNPSJB Pv. 184 or UNPSJB Pv. 612
Zupaysaurus rougieri - Arcucci and Coria (2003)

TABLE 5. Operational Taxonomic Units and their percentage of relative completeness in the taxon-character matrix used in the phylogenetic analyses.

Abelisaurus comahuensis ……..23.1
Allosaurus fragilis …….100
Aucasaurus garridoi ……. 39.8
Baryonyx walkeri …….. 58.0
Camposaurus arizonensis …… 3.4
Carnotaurus sastrei …….. 80.3
Ceratosaurus nasicornis ……... 91.3
Coelophysis bauri ……. 92.8
Dilophosaurus wetherilli …….. 90.2
Elaphrosaurus bambergi …….. 36.7
Eoraptor lunensis ……..72.0
Eustreptospondylus oxoniensis …….48.1
Genusaurus sisteronus ……. 3.4
Gojirasaurus quayi ……... 9.8
Herrerasaurus ischigualastensis ….. 93.2
Ilokelesia aguadagrandensis …… 15.2
Irritator challengeri ……..23.5
Lesothosaurus diagnosticus ……..89.8
Liliensternus liliensterni ……... 46.6
Majungatholus atopus …….. 70.5
Marasuchus lilloensis ……... 51.5
Masiakasaurus knopfleri …….. 41.7
Noasaurus leali ……. 11.7
Ornitholestes hermanni …….63.3
Plateosaurus engelhardti ……..99.6
"Poekilopleuron" valedunensis …… 23.5
Procompsognathus triassicus ……... 14.4
Rugops primus …….. 23.1
Scutellosaurus lawleri …….. 56.1
Segisaurus halli …… 17.1
Shake-N-Bake taxon ……. 39.1
Shuvosaurus inexpectatus ……30.7
Spinostropheus gautieri …… 11.4
Suchomimus tenerensis …….41.7
"Syntarsus" kayentakatae ……. 83.3
Syntarsus rhodesiensis ……..95.1
Torvosaurus tanneri ……. 64.8
Xenotarsosaurus bonapartei …….13.6
Zupaysaurus rougieri ……... 30.7

TABLE 6. Maturity-dependent characters deleted from the analysis in Phylogenetic Test 2. This replicates the approach to 'ontogenetically variable' characters advocated and practiced by Rauhut (2003).

39. Nasals are separate (0), or partially fused, either at anterior end or within median crests or prominences (1), or fused over entire length (2) in adults (modified from Sereno, 1999a). (O)

46. Frontals remain separate (0), or indistinguishably fuse to each other (1) in adults (Holtz, 1998).

48. Frontals and parietals remain separate (0), or fuse (1) in adults (Holtz, 1998; Forster, 1999; Sereno, 1999a).

74. Quadratojugal and quadrate remain separate (0), or fuse (1) in adults (Holtz, 1994, 1998).

130. Cervical ribs remain separate from (0), or co-ossify to (1) their respective vertebral centra in adults (Gauthier, 1986).

150. Sacral centra remain separate or exhibit limited co-ossification (0), or exhibit full fusion to one another so sutures nearly indiscernible (1) by adulthood (modification of Rowe, 1989; Rowe and Gauthier, 1990).

151. Sacral neural arch elements (transverse processes, arches, neural spines) and sacral ribs of adjacent vertebrae remain separate (0), or fuse to one another by adulthood (1) (Rowe, 1989; Rowe and Gauthier, 1990).

152. Sacral transverse process of at least mid-sacrals remain separate (0), or coalesce to form nearly continuous horizontal sheet in dorsal view (1) by adulthood (Rauhut, 2003).

153. Sacral ribs and transverse processes remain separate (0), or fuse to ilia (1) in adults (Rowe 1989; Rowe and Gauthier, 1990).

167. Anterior margin of scapulocoracoid at scapula-coracoid contact notched (0), or continuous and uninterrupted (1) in adults (Holtz, 1998).

189. Pelvic bones remain separate (0), or co-ossify with one another (1) by adulthood (Rowe, 1989; Rowe and Gauthier, 1990).

210. Distal tip of pubis lacking substantial anteroposterior enlargement (0), or enlarged 2<3 times (1) or ≥3 times (2) anteroposterior width of pubic shaft (modified from Rauhut, 2003). (O)

221. Femoral dimorphism not present (0), or present, expressed in muscle scars, attachments, and processes ('robust' versus 'gracile' morphs) (1) (Rowe and Gauthier, 1990).

222. Femoral anterior trochanter a low ridge or tuberosity (0), or a conical spike or pyramidal prominence (1), or a mediolaterally compressed flange (=aliform process) projecting anteriorly from femur (2) (modified from Gauthier, 1986; Carrano, 2000). (UO)

224. Femoral trochanteric shelf large and pronounced (0), or expressed as low mound or swelling distolateral to anterior trochanter (1) in adults (modified from Carrano et al., 2002).

225. Medial epicondyle of femur weak (0), or strongly developed ridge (1), or hypertophied and flange-like (2) (Forster, 1999). (O)

226. Anterior surface of femoral distal end flat or convex (0), or with broad, shallow, depression bordered medially by medial epicondyle (1) in adults (Rauhut, 2003).

227. Tibiofibular crest of femur smoothly continuous with lateral distal condyle (0), or sharply demarcated from lateral distal condyle by sulcus or concavity (1) (Rowe, 1989).

228. Femoral popliteal fossa smooth (0), or traversed by infrapopliteal ridge between medial (=tibial) distal condyle and tibiofibular crest (1) in adults (Tykoski 1998).

237. Medial side of proximal end of fibula flat (0), or excavated by longitudinal groove (1) (modified from Rowe, 1989; Rowe and Gauthier, 1990; Rauhut, 2003).

238. Medial side of proximal end of fibula flat (0), or with oblique (posteroproximal to anterodistal) ridge that overlaps proximal part of medial fibular groove (1) (Rowe, 1989; Rowe and Gauthier, 1990; Rauhut, 2003).

241. Fibula does not overlap astragalus (0), or bears medial flange that overlaps part of the ascending process of astragalus (1) (Rowe, 1989; Rowe and Gauthier, 1990).

242. Fibula separate from (0), or co-ossifies with (1) ascending process of astragalus of adults (Carrano et al., 2002).

249. Astragalus and calcaneum remain separate (0), or fuse to each other (1) by adulthood (Rowe 1989).

250. Astragalus and tibia remain separate (0), or fuse to each other (1) by adulthood (Rowe, 1989).

252. Distal tarsal III remains separate (0), or fuses to (1) metatarsal III by adulthood (modified from Rowe, 1989; Rowe and Gauthier, 1990).

257. Proximal ends of metatarsals II and III remain separate (0), or co-ossify to each other (1) by adulthood (Rowe, 1989).

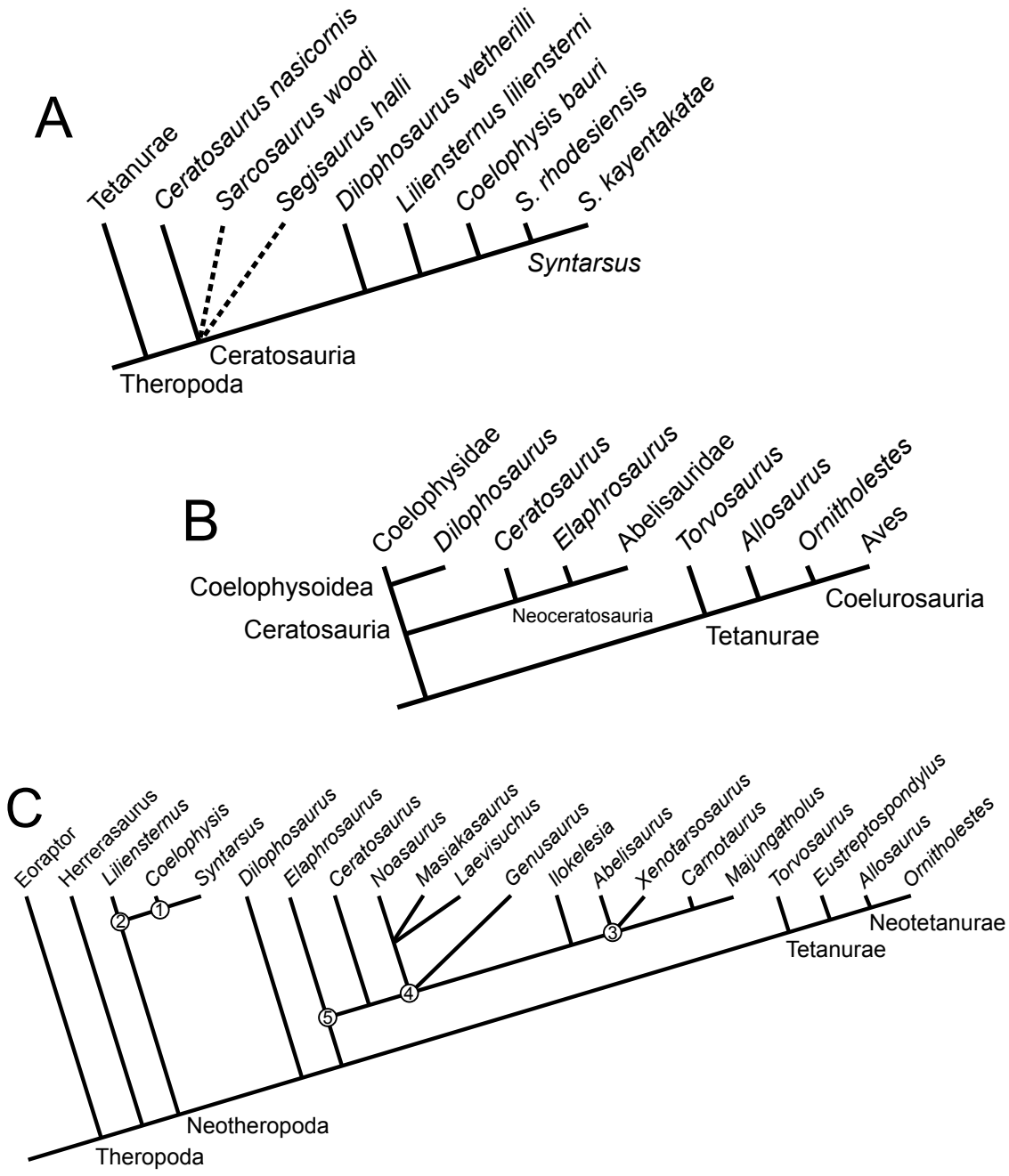


FIGURE 1. Hypotheses of basal theropod phylogeny. A, Rowe (1989); B, Holtz (1994); C, Carrano et al., (2002). Numbered clades in C reflect clade nomenclature of Carrano et al., (2002), and are as follows: 1, Coelophysinae; 2, Coelophysidae; 3, Abelisauridae; 4, Abelisauroidea; 5, Neoceratosauria.

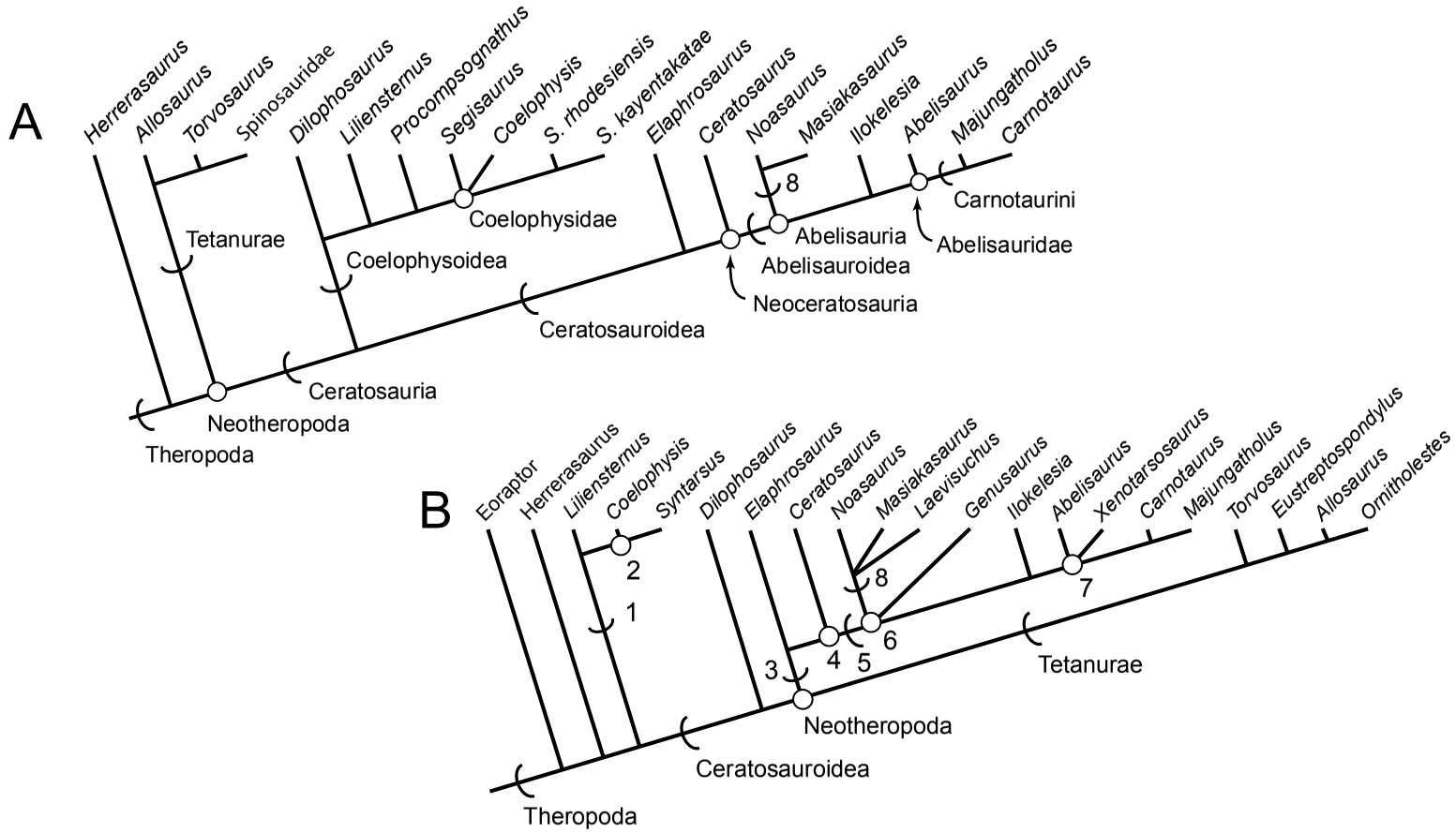


FIGURE 2. Distribution of clade names as defined and used here. A, based upon phylogenetic hypothesis of Holtz (1998). B, based upon phylogenetic hypothesis of Carrano et al., (2002). Open circles denote node-based clade names. Arcs indicate stem-based clade names. Key to numbered clades: 1, Coelophysoidea; 2, Coelophysidae; 3, Ceratosauria; 4, Neoceratosauria; 5, Abelisauroidea; 6, Abelisauria; 7, Abelisauridae; 8, Noasauridae.

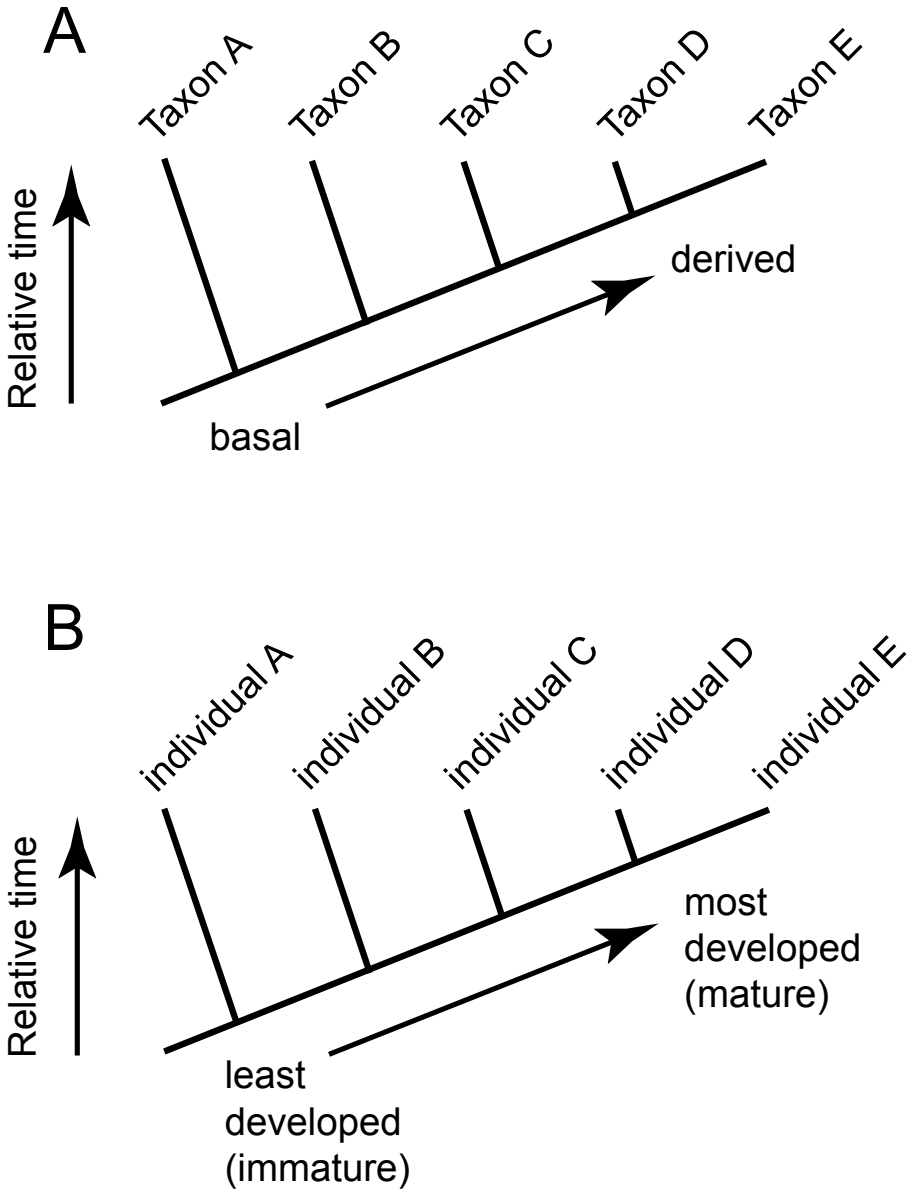


FIGURE 3. Cladogram versus ontogram. Figure illustrates the different data visually relayed by A, a cladogram, and B, an ontogram.

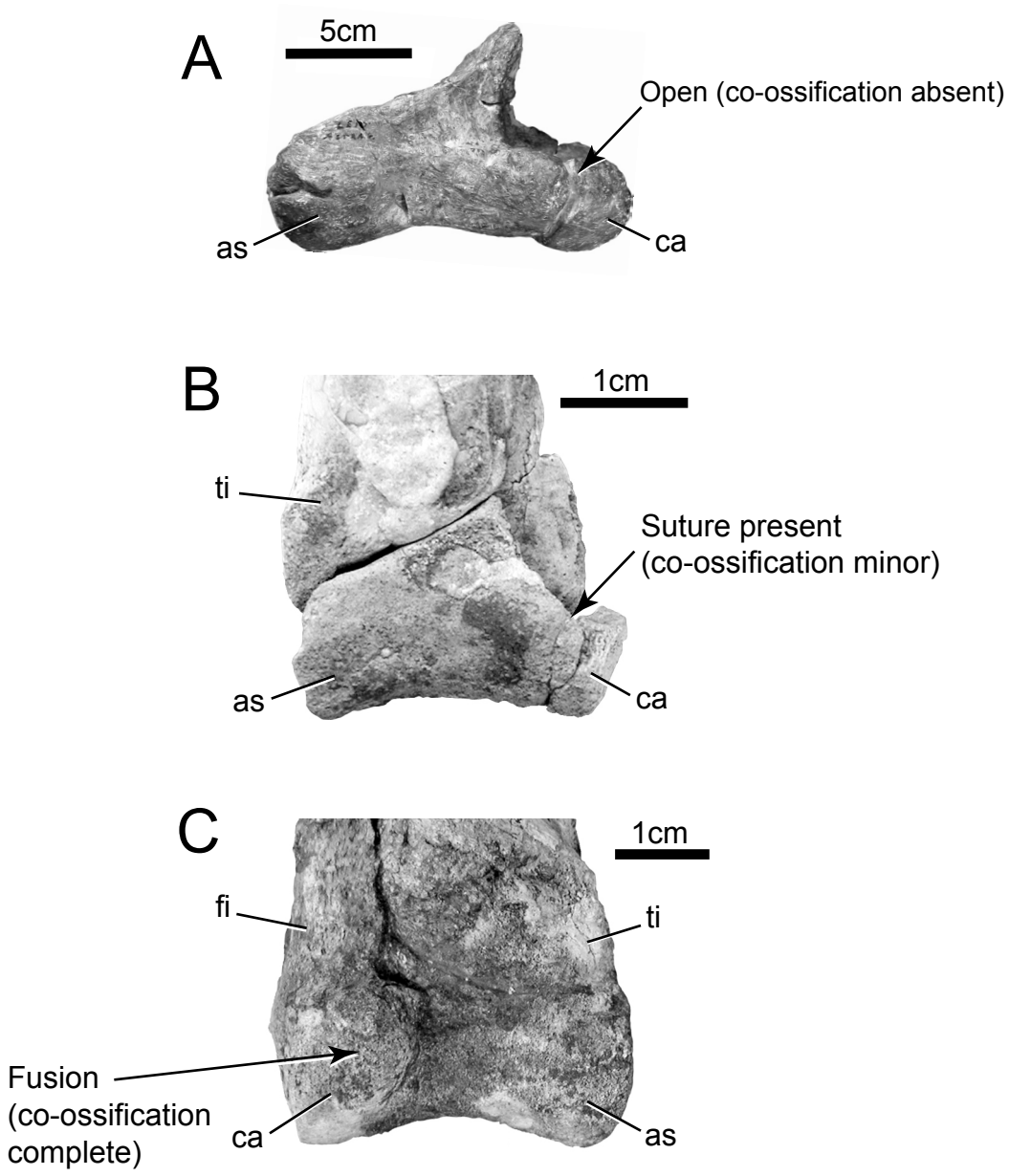


FIGURE 4. Coelophysoid proximal tarsals and tibia. Astragalus-calcaneum contact illustrates the three states of co-ossification coded in the ontogenetic analysis. A, UCMP 37302 *Dilophosaurus wetherilli*, open contact. B, TMM 43669-3 "*Syntarsus" kayentakatae*, suture present but still visible. C, MNA V2623 "*Syntarsus" kayentakatae*, fusion present and suture obliterated. All anterior view.

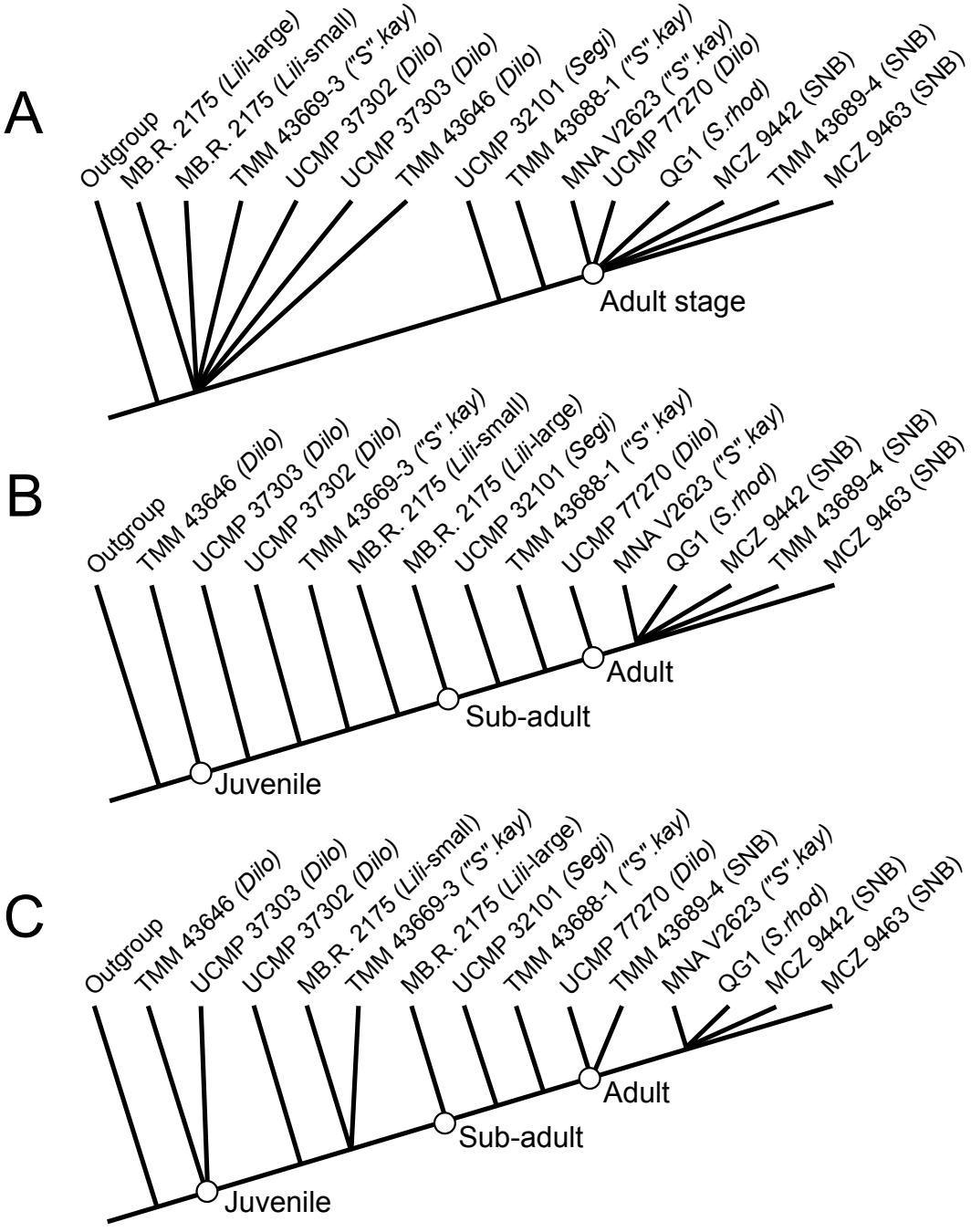


FIGURE 5. Consensus ontograms from 3645 equally most parsimonious hypotheses of relative ontogenetic development (L=81, C.I.=0.9259. R.I.=0.9531). A, strict consensus ontogram. B, 50% majority rule consensus ontogram. C, Adams consensus ontogram. *Dilo=Dilophosaurus*, *Lili=Liliensternus*, *S.kay="Syntarsus" kayentakatae*, *S.rhod=Syntarsus rhodesiensis*, SNB=Shake-N-Bake taxon.

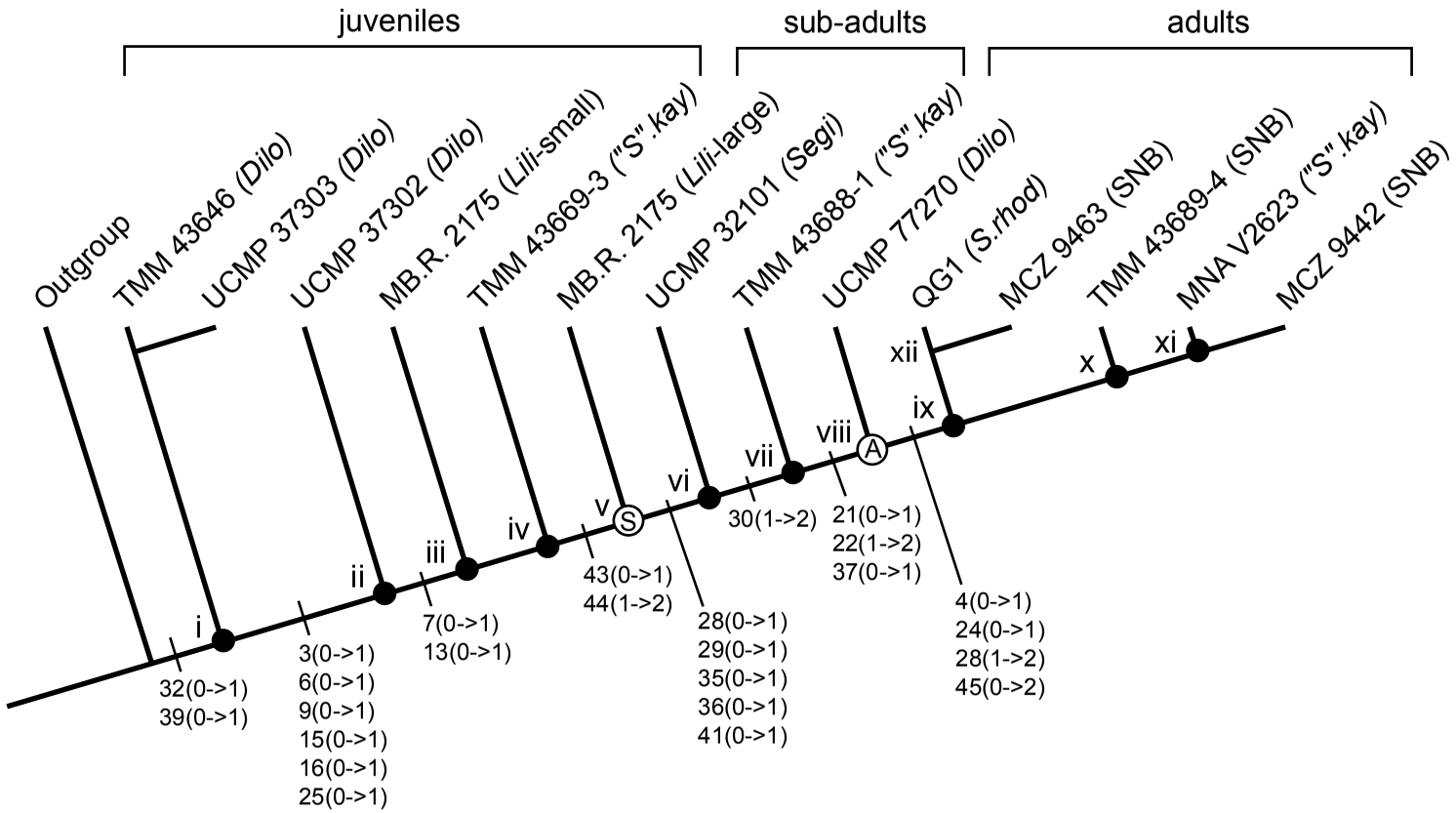


FIGURE 6. One of 3645 equally most parsimonious ontograms depicting relative ontogenetic development expressed in remains of 14 individuals from five coelophysoid taxa. Hypothetical all-zero outgroup. Length = 81, C.I.=09259, R.I.=0.9531. Sub-adult and adult stages minimum boundary nodes indicated by open circles. Unambiguous characters listed for each node. Complete list of characters at nodes with roman numerals listed on Table 3. Name abbreviations as in Figure 5.

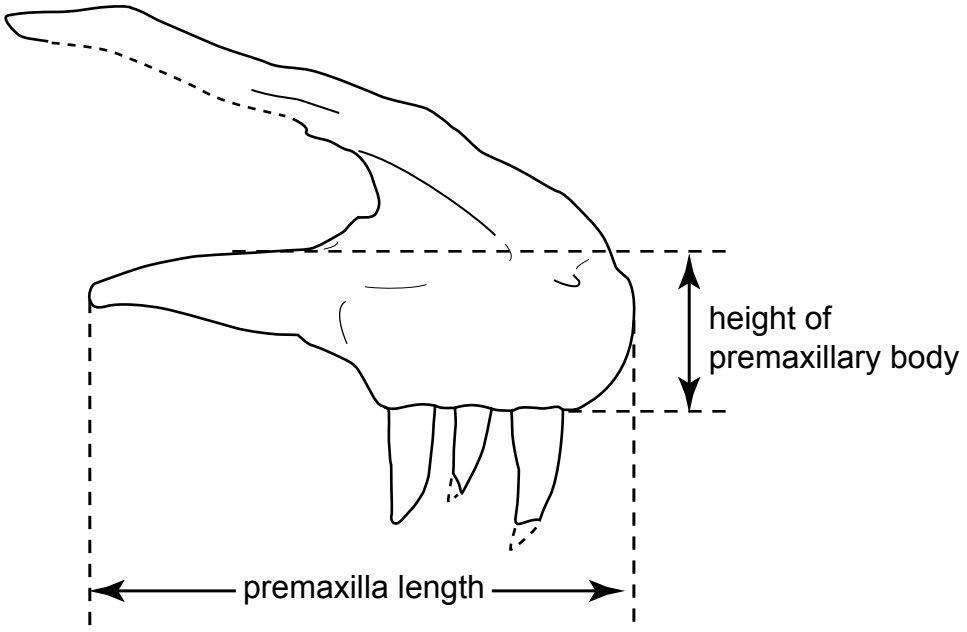


FIGURE 7. Premaxillary body height versus length ratio. In this example, the height of the premaxilla below the external naris is 22mm and the length of the premaxilla is 72mm. This yields a height to length ratio of 22mm/72mm=0.3055. Specimen is not to scale.

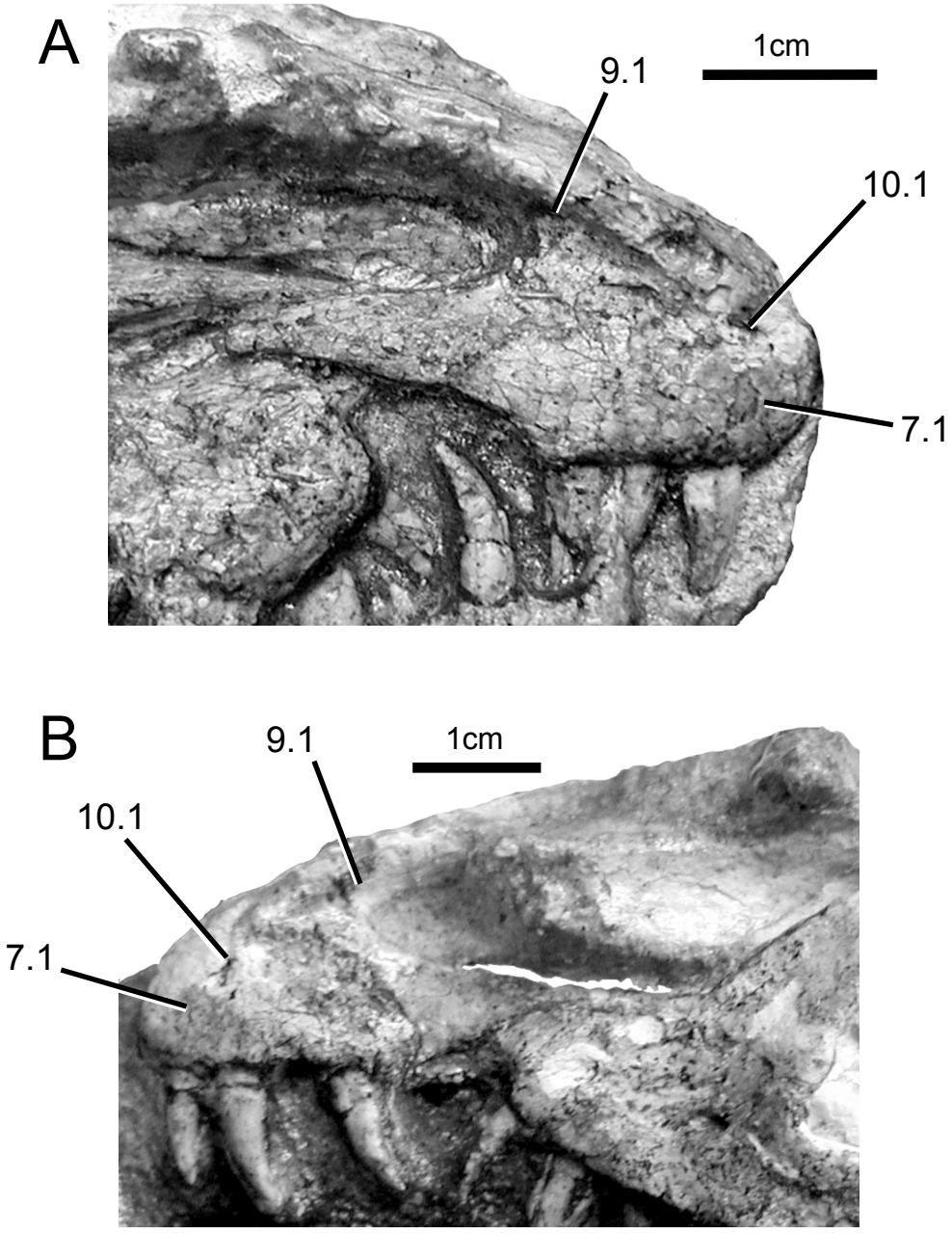


FIGURE 8. *"Syntarsus" kayentakatae (*MNA V2623) anterior rostrum. A, right side, lateral view. B, left side, lateral view.

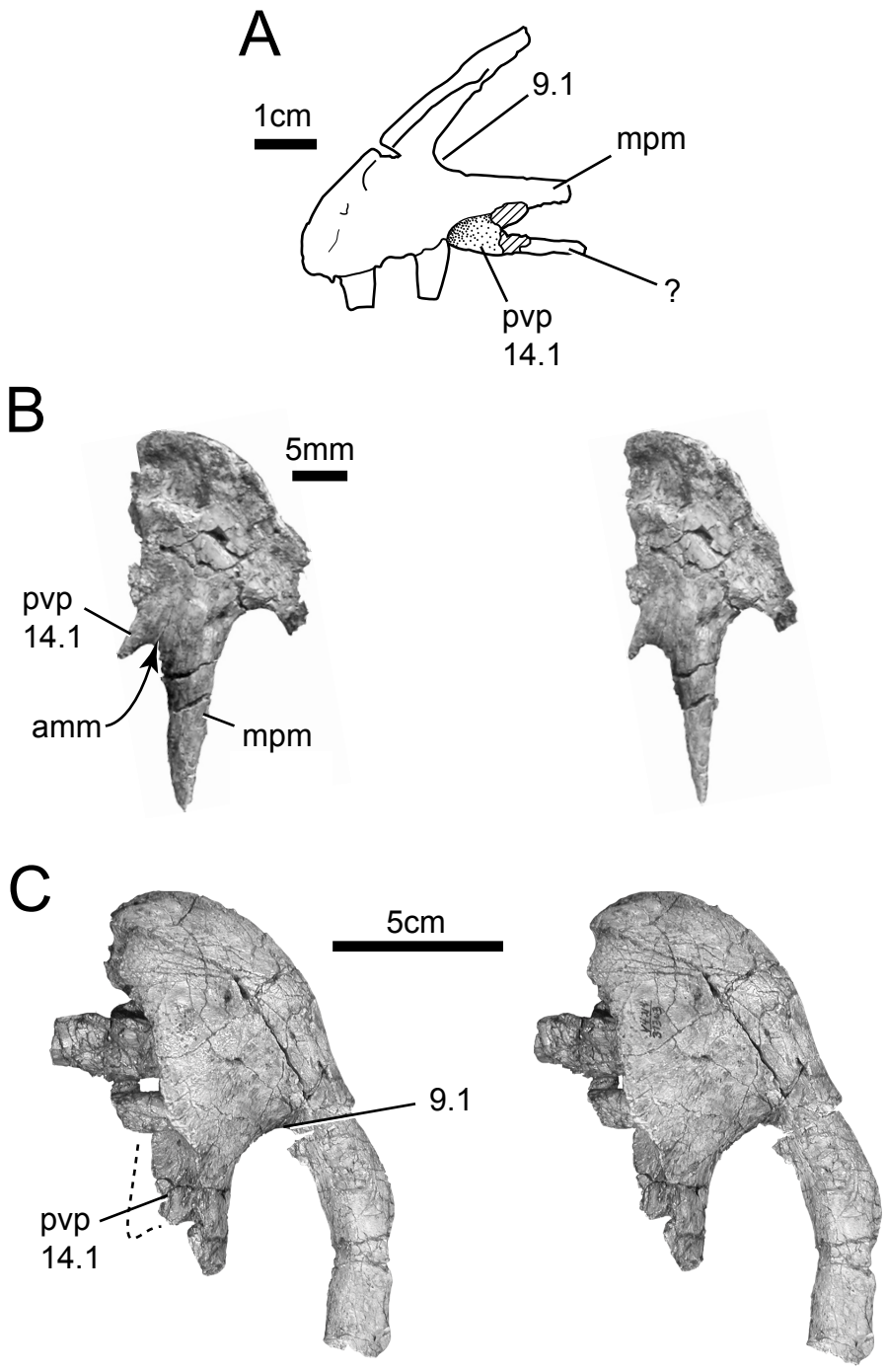


FIGURE 9. Coelophysoid premaxillae. A, *Syntarsus rhodesiensis* left premaxilla, lateral view (after Rauhut, 2003); B, "*Syntarsus" kayentakatae* (MNA V2623) 'paratype' specimen, stereophotopair of right premaxilla, medial view; C, *Dilophosaurus* (UCMP 37303), stereophotopair of left premaxilla, lateral view. B and C, anterior to top.

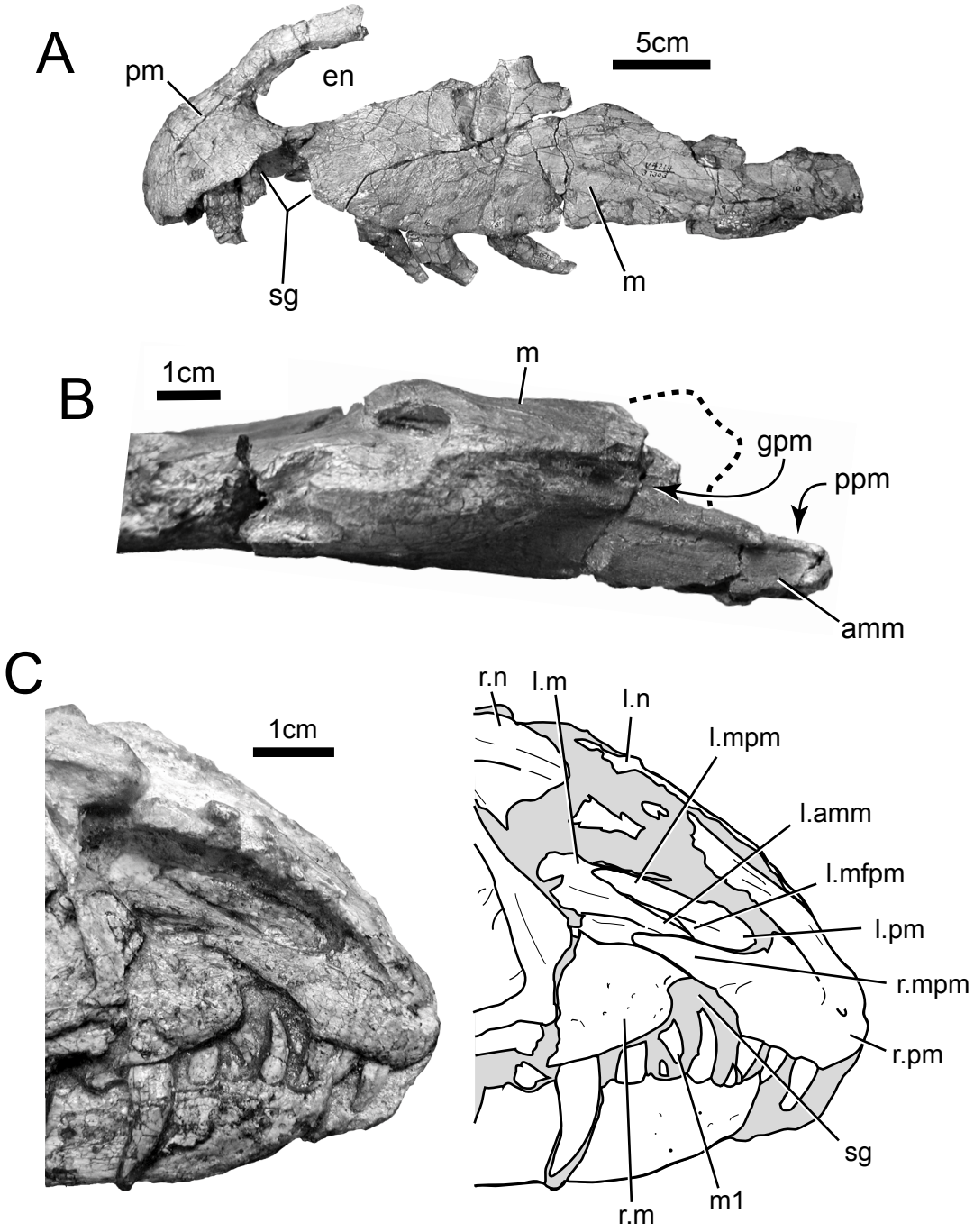


FIGURE 10. Premaxilla-maxilla contact. A, *Dilophosaurus wetherilli* (UCMP 37303) left premaxilla and maxilla, lateral view. B, *Dilophosaurus wetherilli* (TMM 43646-1) anterior end of left maxilla, dorsal view. C, *"Syntarsus" kayentakatae* (MNA V2623) anterior part of skull, right lateral view.

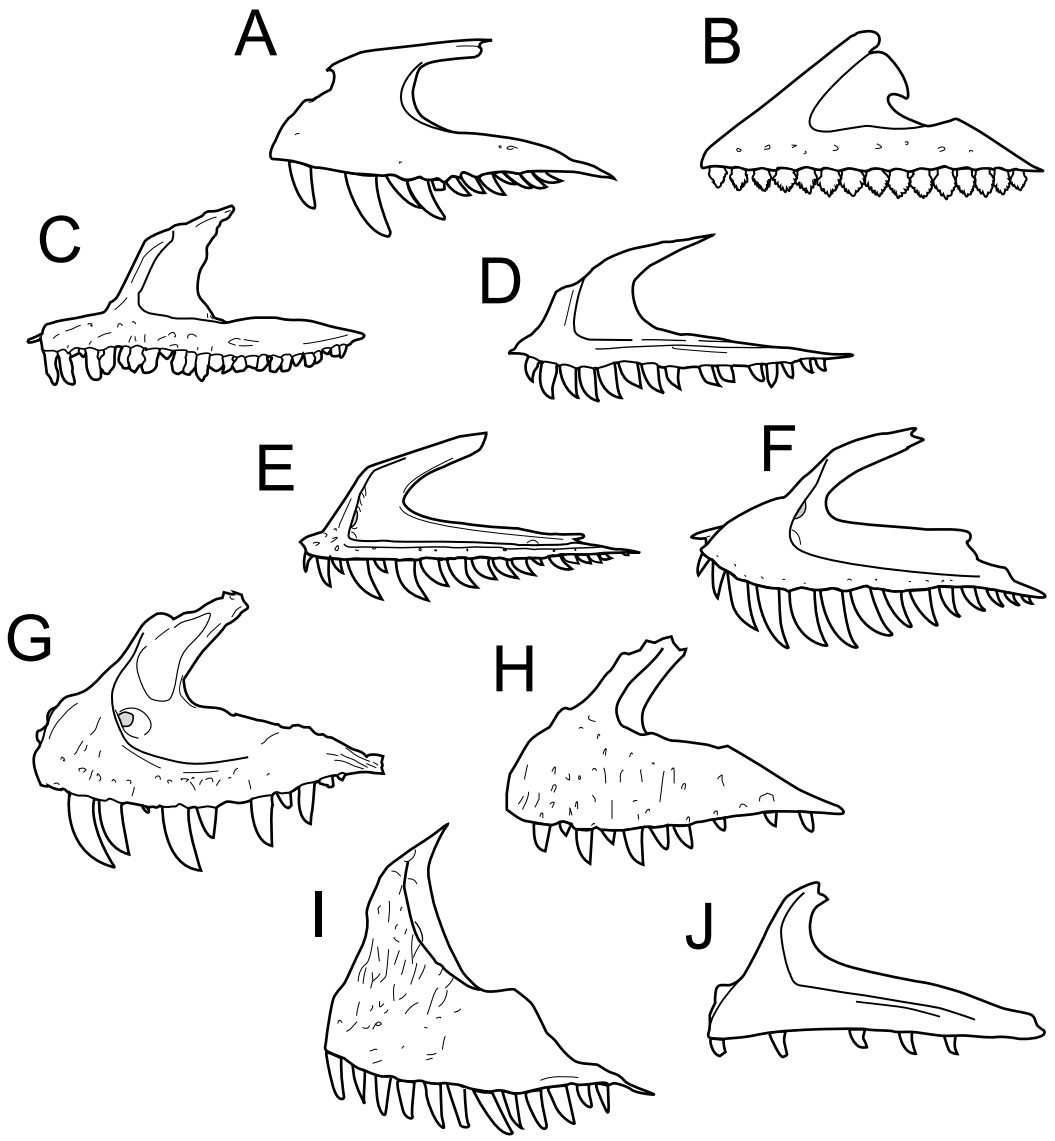


FIGURE 11. Dinosaur maxillae. A, *Herrerasaurus* (after Sereno and Novas, 1993). B, *Lesothosaurus* (after Sereno, 1991). C, *Plateosaurus* (AMNH 6810; after Galton, 1984b). D, *Eoraptor* (PSVJ 512, reversed). E, *"Syntarsus" kayentakatae* (MNA 2623). F, *Dilophosaurus* (composite of UCMP 37302, 37303, TMM 43646, and inspection of UCMP 77270). G, *Ceratosaurus* (UUVP VP5278; Rauhut, 2003). H, *Majungatholus* (FMNH PR 2100; after Sampson et al., 1998). I, *Carnotaurus* (after Bonaparte et al., 1990). J, *Noasaurus* (after Bonaparte, 1991; reversed). All maxillae drawn to same anteroposterior length, not to scale.

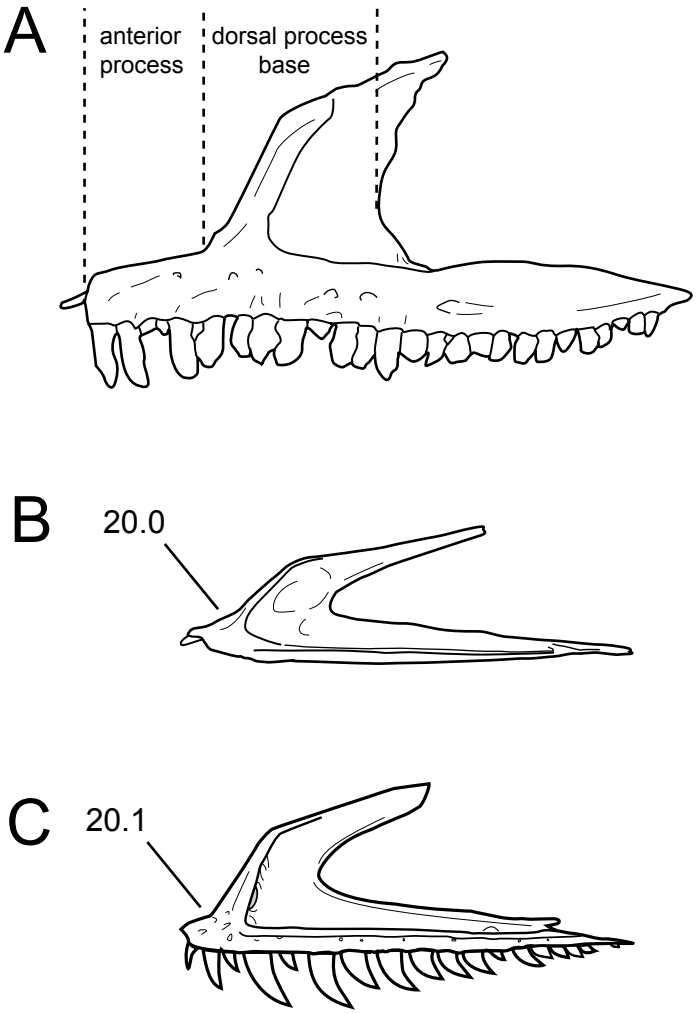


FIGURE 12. Anterodorsal border of the maxilla. A, *Plateosaurus* (AMNH 6810; after Galton, 1984b), showing reference points used to define extent of maxillary anterior process and dorsal process. B, *Syntarsus rhodesiensis* (QG194; after Raath, 1977), example of gradual transition from anterior to dorsal process. C, *"Syntarsus" kayentakatae* (MNA V2623), example of an abrupt, 'kinked', or angular transition from anterior to dorsal process. Drawings not to scale.

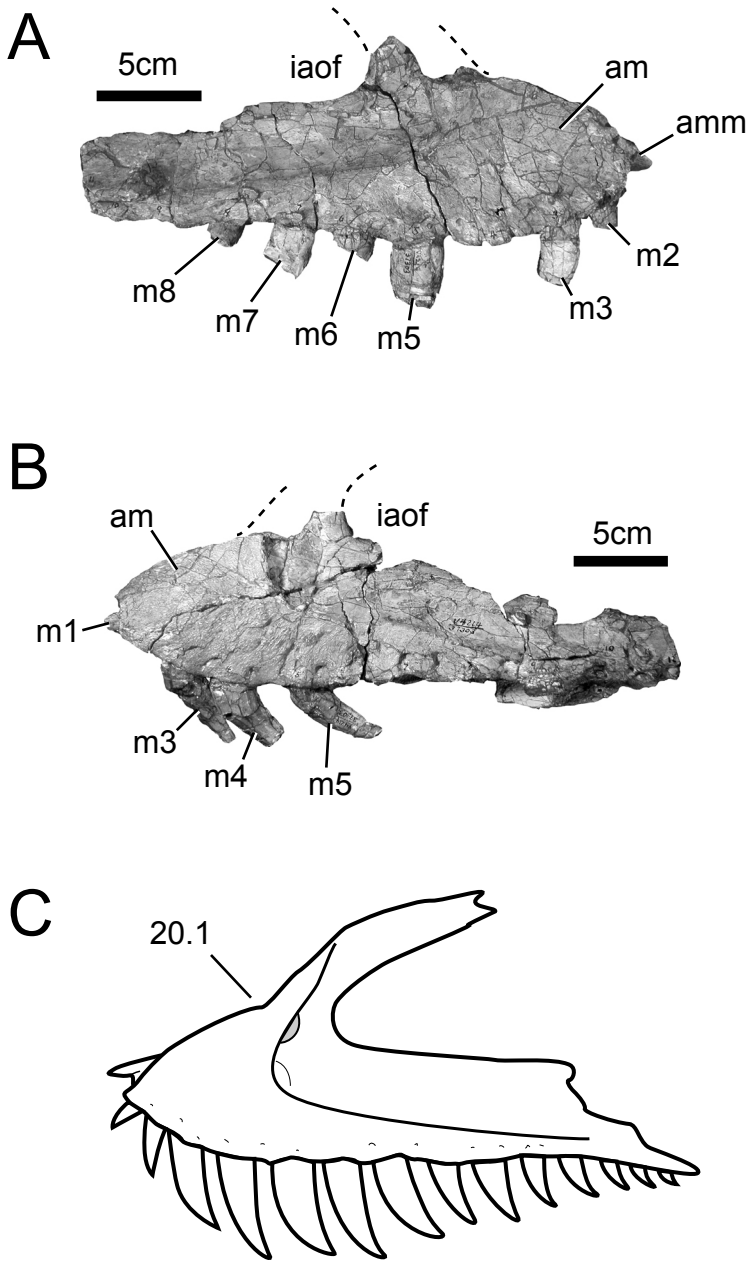


FIGURE 13. Maxillae of *Dilophosaurus*. A, UCMP 37303 right maxilla in lateral view. B, UCMP 37303 left maxilla in lateral view. Dashed lines indicate borders of base of dorsal process. C, reconstruction of *D. wetherilli* maxilla based upon UCMP 37302, UCMP 37303, TMM 43646-1, and visual inspection of UCMP 77270.

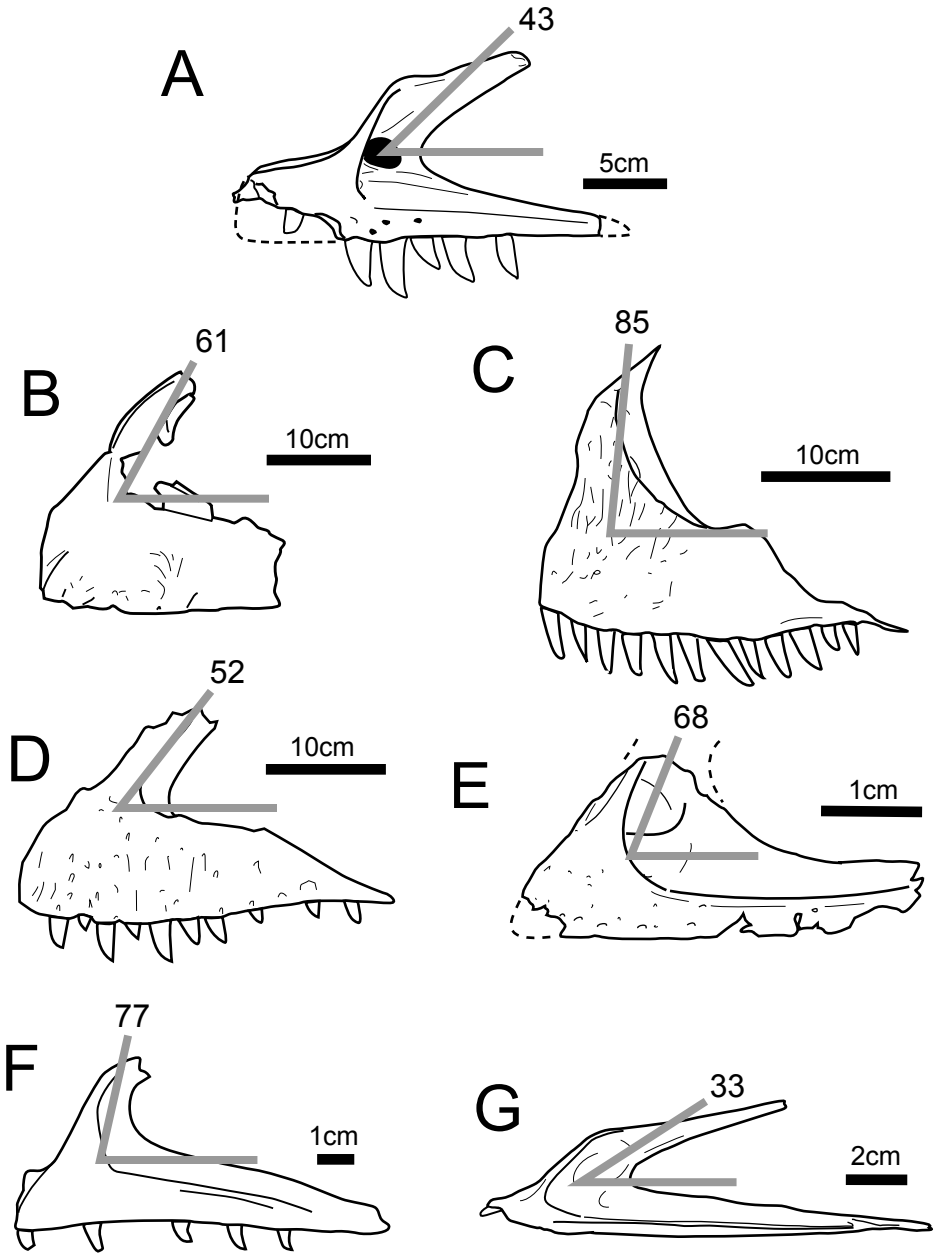


FIGURE 14. Maxillary dorsal process angle from horizontal. A, *Poekilopleuron? valedunensis* (reversed-after Allain, 2002); B *Abelisaurus* (after Bonaparte and Novas, 1985); C, *Carnotaurus* (after Bonaparte et al., 1990); D, *Majungatholus* (after Sampson et al., 1998); E, *Masiakasaurus* (reversed-after Carrano et al., 2002); F, *Noasaurus* (reversed-after Bonaparte, 1991); G, *Syntarsus rhodesiensis* (after Raath, 1977).

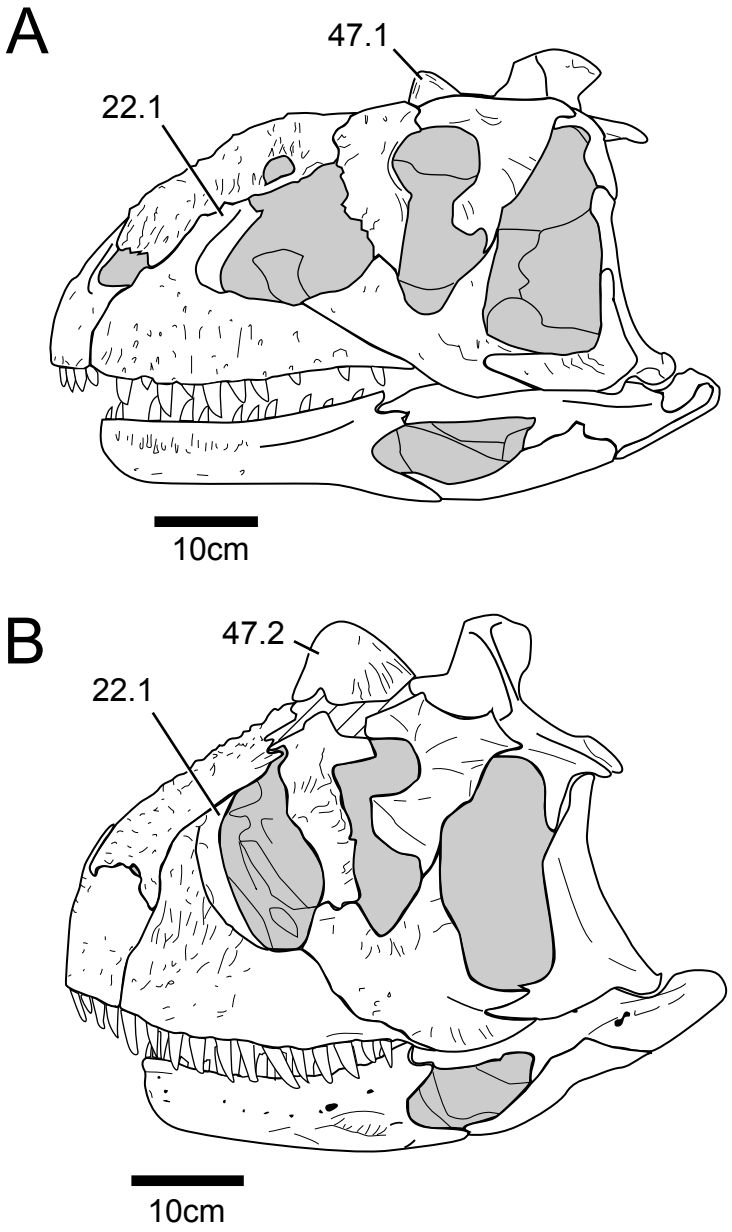


FIGURE 15. Abelisaurid skulls. A, *Majungatholus atopus* (FMNH PR 2100) (after Sampson et al., 1998). B, *Carnotaurus sastrei* (MACN-CH 894) (after Bonaparte et al., 1990). Note the short maxillary dorsal process that does not contact lacrimal.

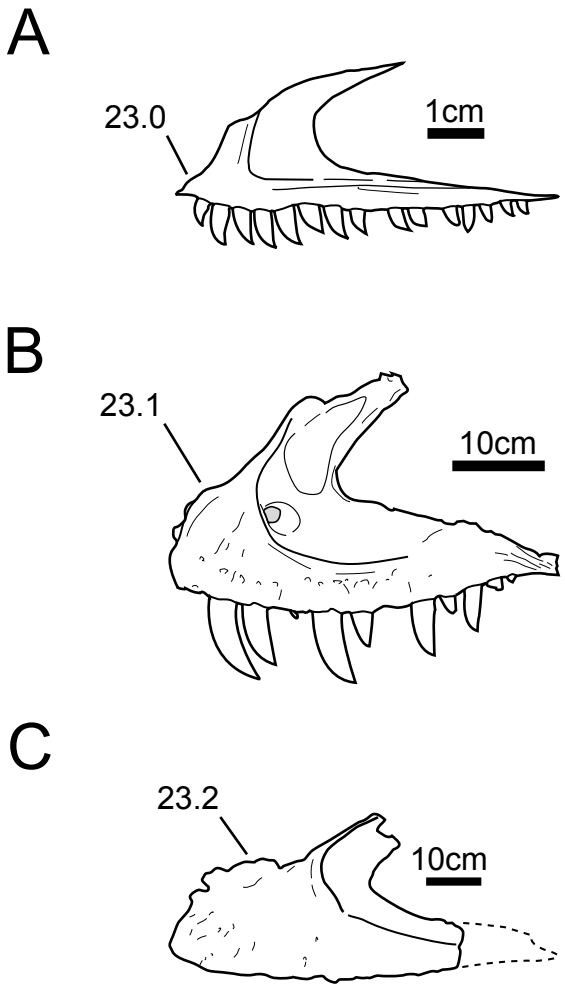


FIGURE 16. Anterior process of theropod maxillae. Figure illustrates different states accounting for the relative anteroposterior length of the anterior process of the maxilla. A, *Eoraptor* (PVSJ 512); B, *Ceratosaurus* (UUVP VP 5278, after Rauhut, 2003); C, *Torvosaurus* (BYU 9122, after Britt, 1991).

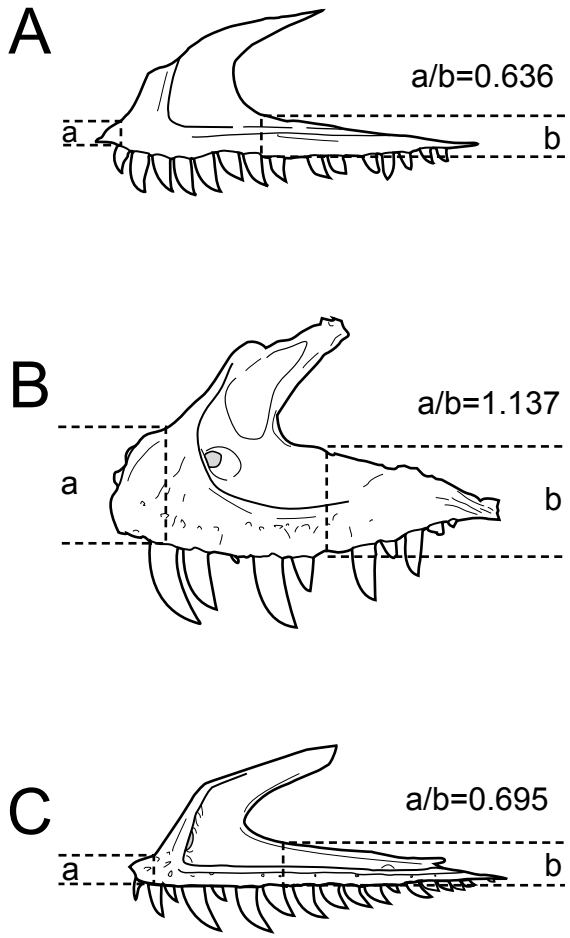


FIGURE 17. Anterior process of theropod maxillae, dorsoventral proportions. Measurement "a" is height of anterior ramus at plane through inflection point along anterodorsal border. Measurement "b" is height of alveolar ramus at plane through posterior margin of first alveolus fully posterior to rim of internal antorbital fenestra. A, *Eoraptor* (PVSJ 512); B, *Ceratosaurus* (UUVP VP5278), after Rauhut, 2003); C, *"Syntarsus" kayentakatae* (MNA V2623). Not to scale.

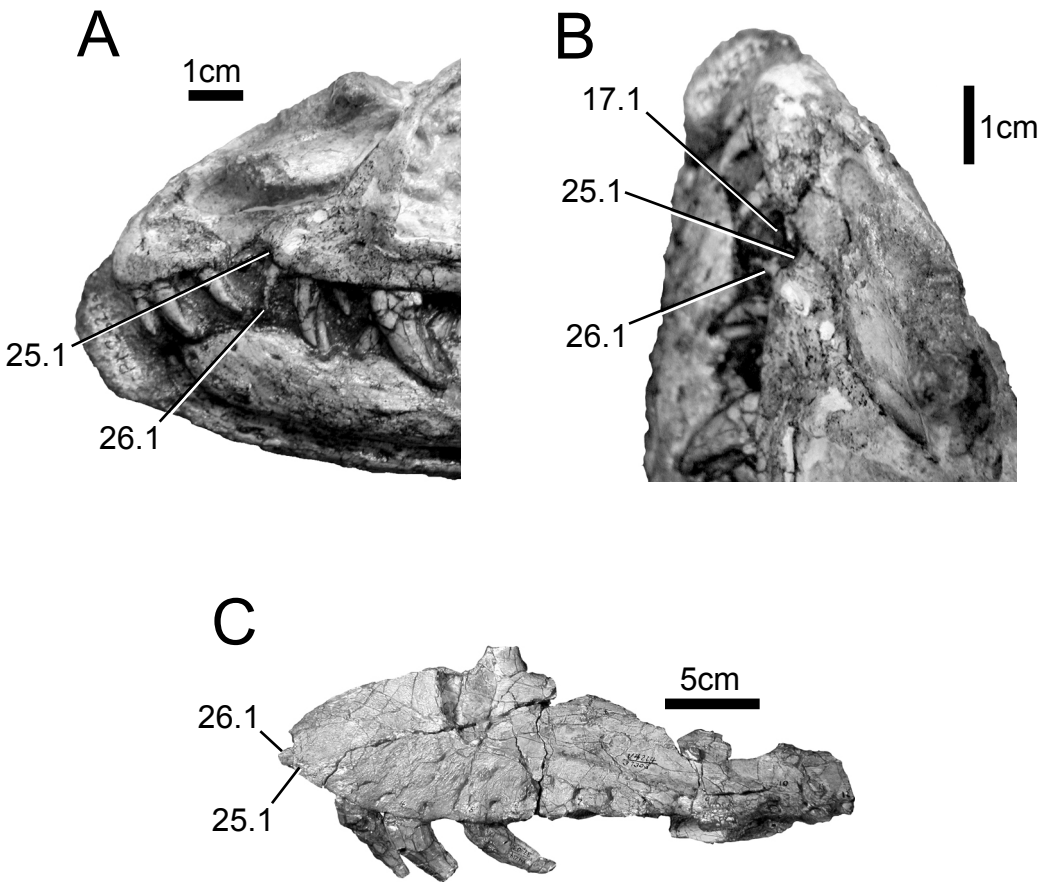


FIGURE 18. Dorsomedially upcurved anterior maxilla. A, *"Syntarsus" kayentakatae* (MNA V2623) anterior end of rostrum, left lateral view. B, same as in A, dorsal and slightly lateral view. C, *Dilophosaurus* (UCMP 37303) left maxilla, lateral view.

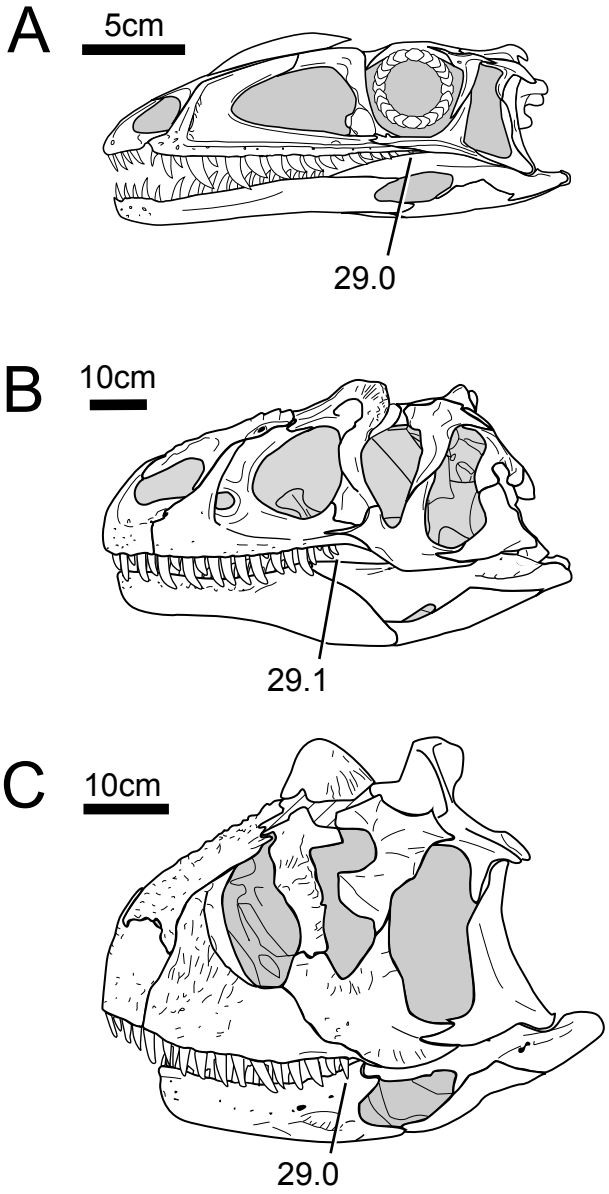


FIGURE 19. Last maxillary tooth position. Tooth row termination relative to the anterior rim of orbit. A, *"Syntarsus" kayentakatae* (MNA V2623) (after Tykoski 1998, Tykoski and Rowe, 2004). B, *Allosaurus* (after Madsen, 1976). C, *Carnotaurus* (MACN-CH 894) (after Bonaparte et al., 1990).

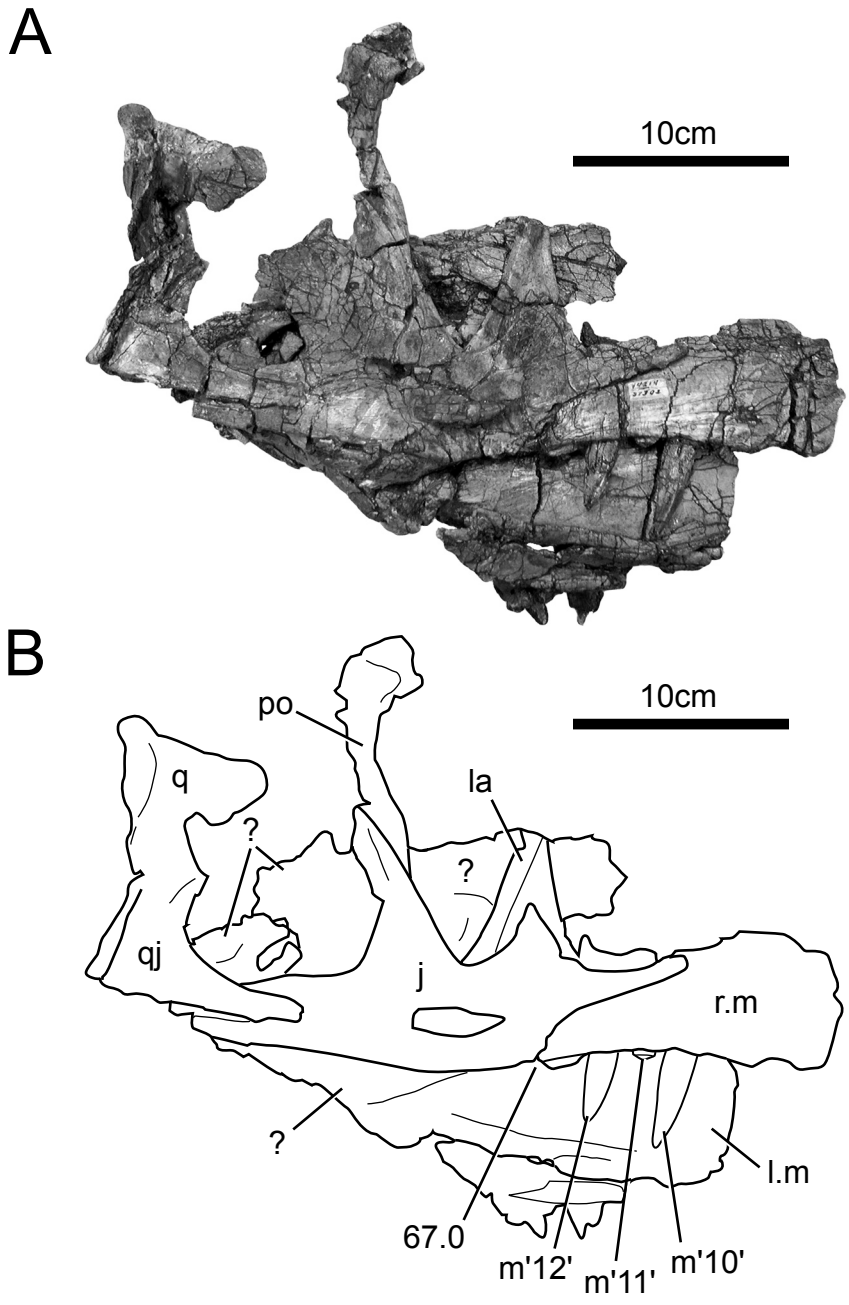


FIGURE 20. *Dilophosaurus* (UCMP 37302) partial skull. A, photo of skull in right lateral view. B, line drawing of A. Note posterior-ward displacement of lacrimal relative to jugal, and the resulting false appearence of a pointed ventral rim of the orbital opening.

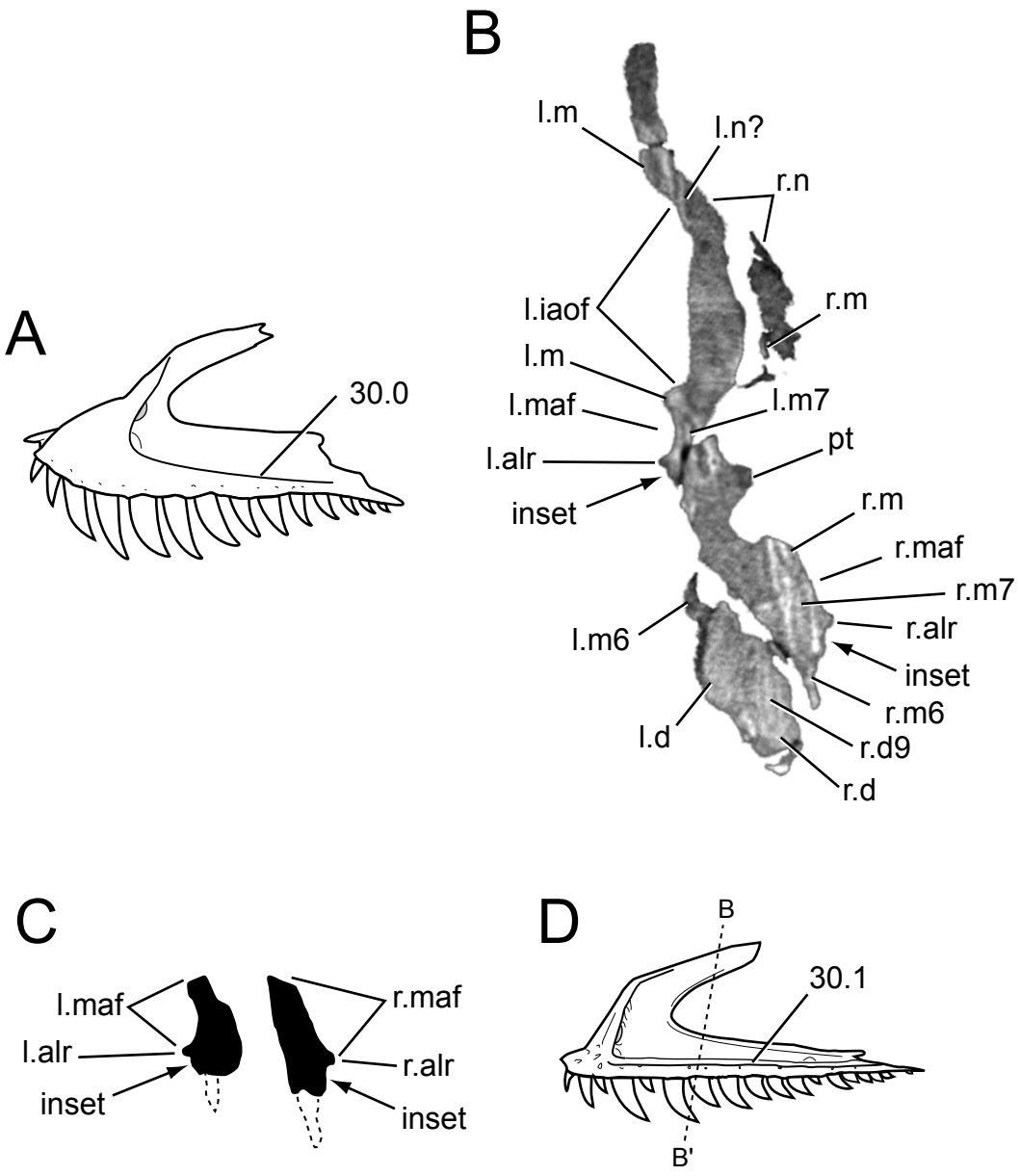


FIGURE 21. Alveolar ridge. A, *Dilophosaurus wetherilli*, alveolar ridge absent, rim of maxillary antorbital fossa dips posteroventrally toward alveolar margin. B, *"Syntarsus" kayentakatae* (MNA V2623) CT scan near-transverse section through rostrum. C, *"Syntarsus" kayentakatae* (MNA V2623) cross sections of maxillae as seen in B. D, *"Syntarsus" kayentakatae* (MNA V2623) outline of left maxilla showing derived state of alveolar ridge and approximate position (B-B') of CT scan slice in B.

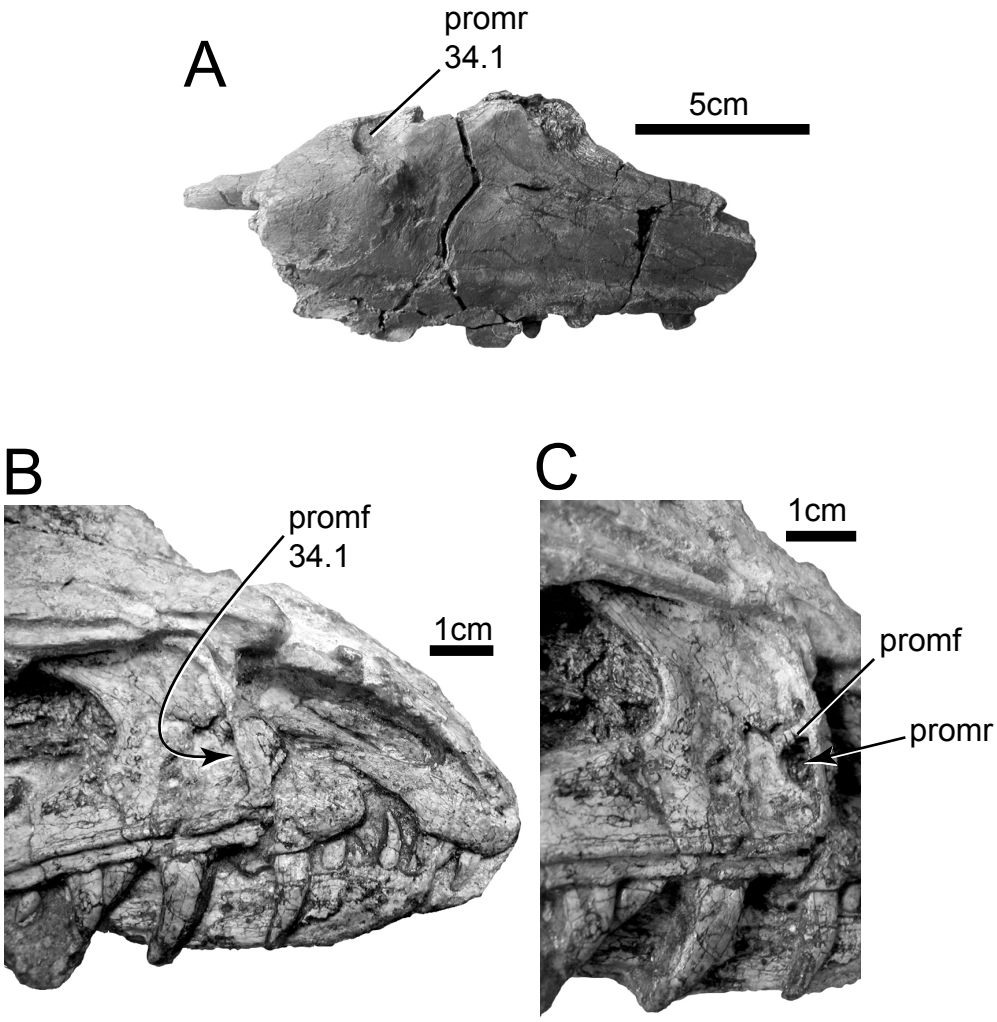


FIGURE 22. Promaxillary fenestra and recess. A, *Dilophosaurus* (TMM 43646-1), partial left maxilla in lateral view. Most of lateral maxillary lamina and dorsal process missing. B, *"Syntarsus" kayentakatae* (MNA V2623), rostrum in right lateral view. C, *"Syntarsus" kayentakatae* (MNA V2623), close-up of anterior part of right maxillary antorbital fossa, posterolateral view.

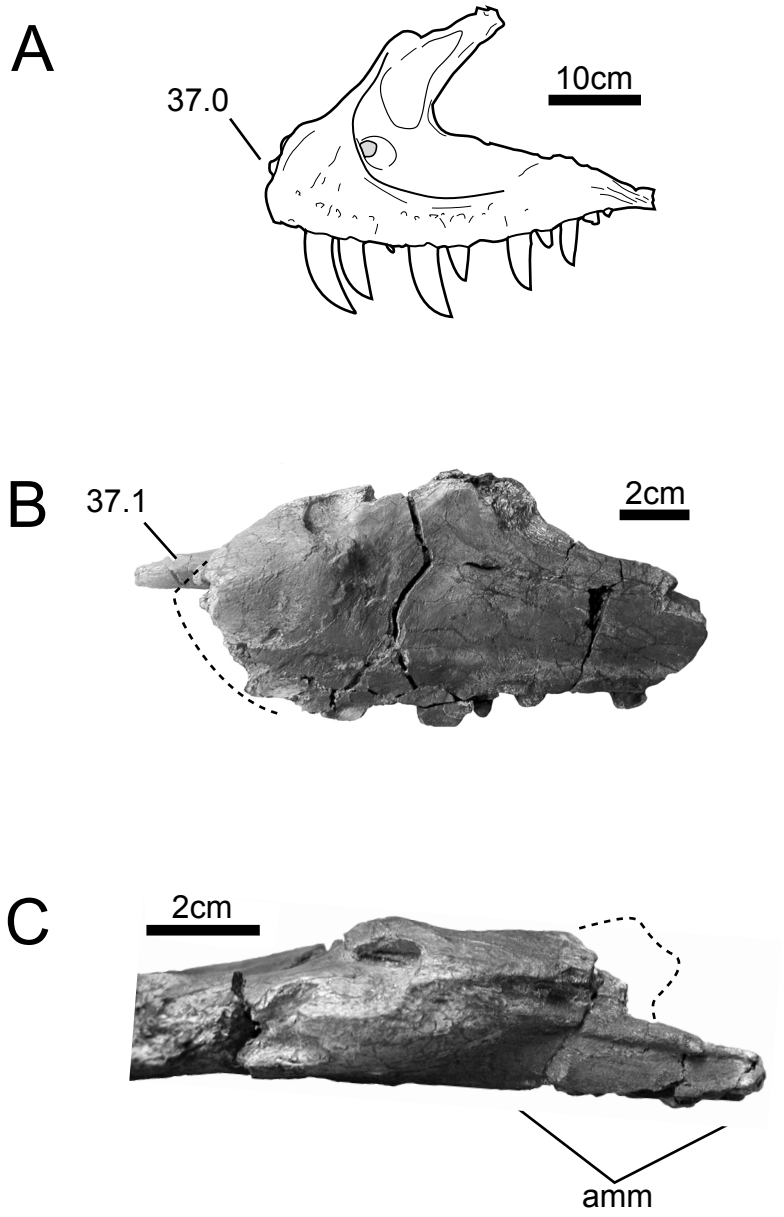


FIGURE 23. Anteromedial process of maxilla relative length. A, *Ceratosaurus* (UUVP VP 5278) maxilla, lateral view. B, *Dilophosaurus* (TMM 43646-1), left maxilla, lateral view. Note protruding anteromedial process. C, *Dilophosaurus* (TMM43646-1) left maxilla, dorsal view. Dashed lines indicate projected outline of bone margin.

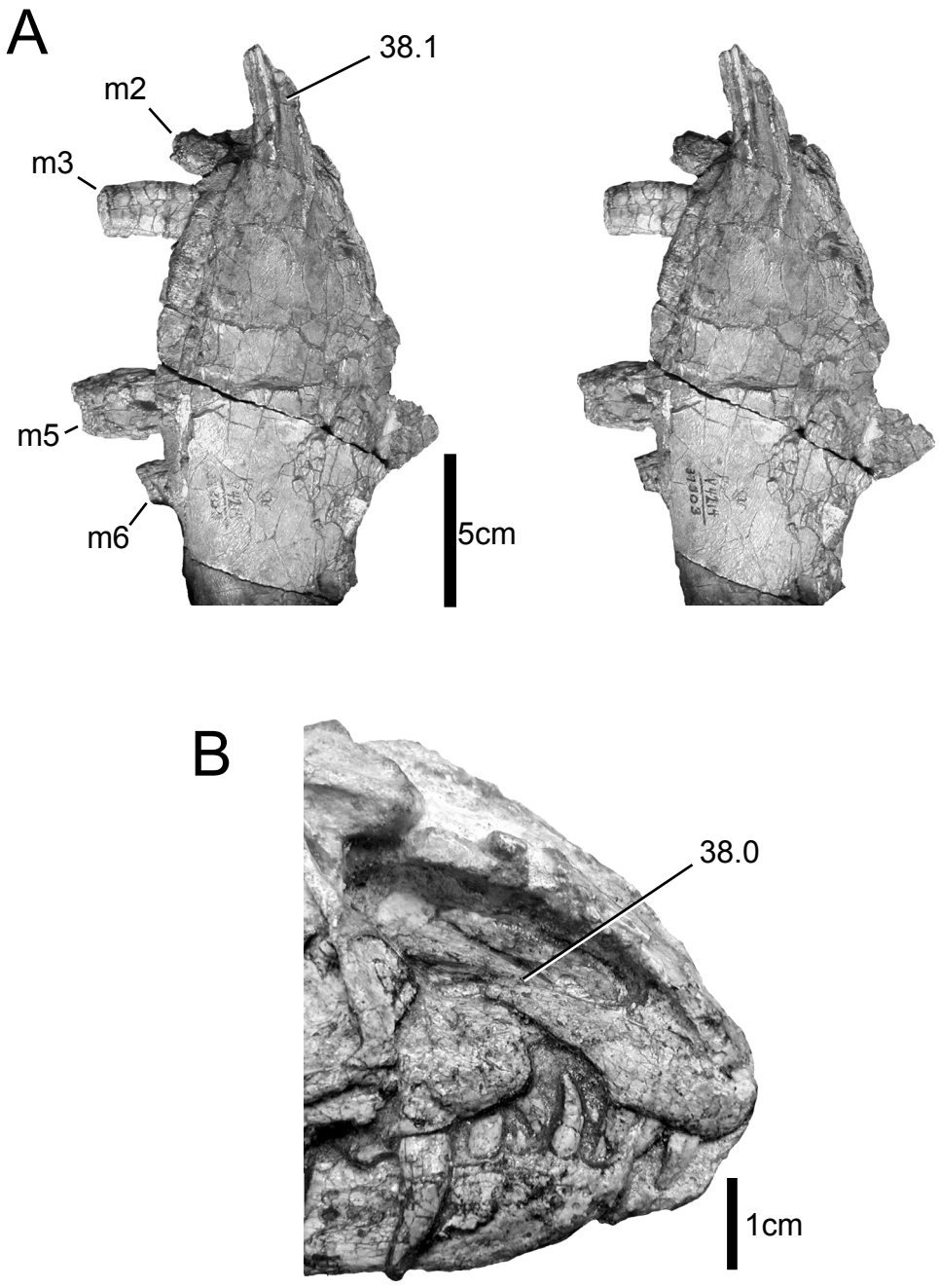


FIGURE 24. Anteromedial process medial ridges. A, *Dilophosaurus* (UCMP 37303) stereopair of anterior half of right maxilla, medial view. B, *"Syntarsus" kayentakatae* (MNA V2623), rostrum in right lateral view, looking at medial surface of anteromedial process of left maxilla. See Fig. 9C for additional anatomical identifications in this area.

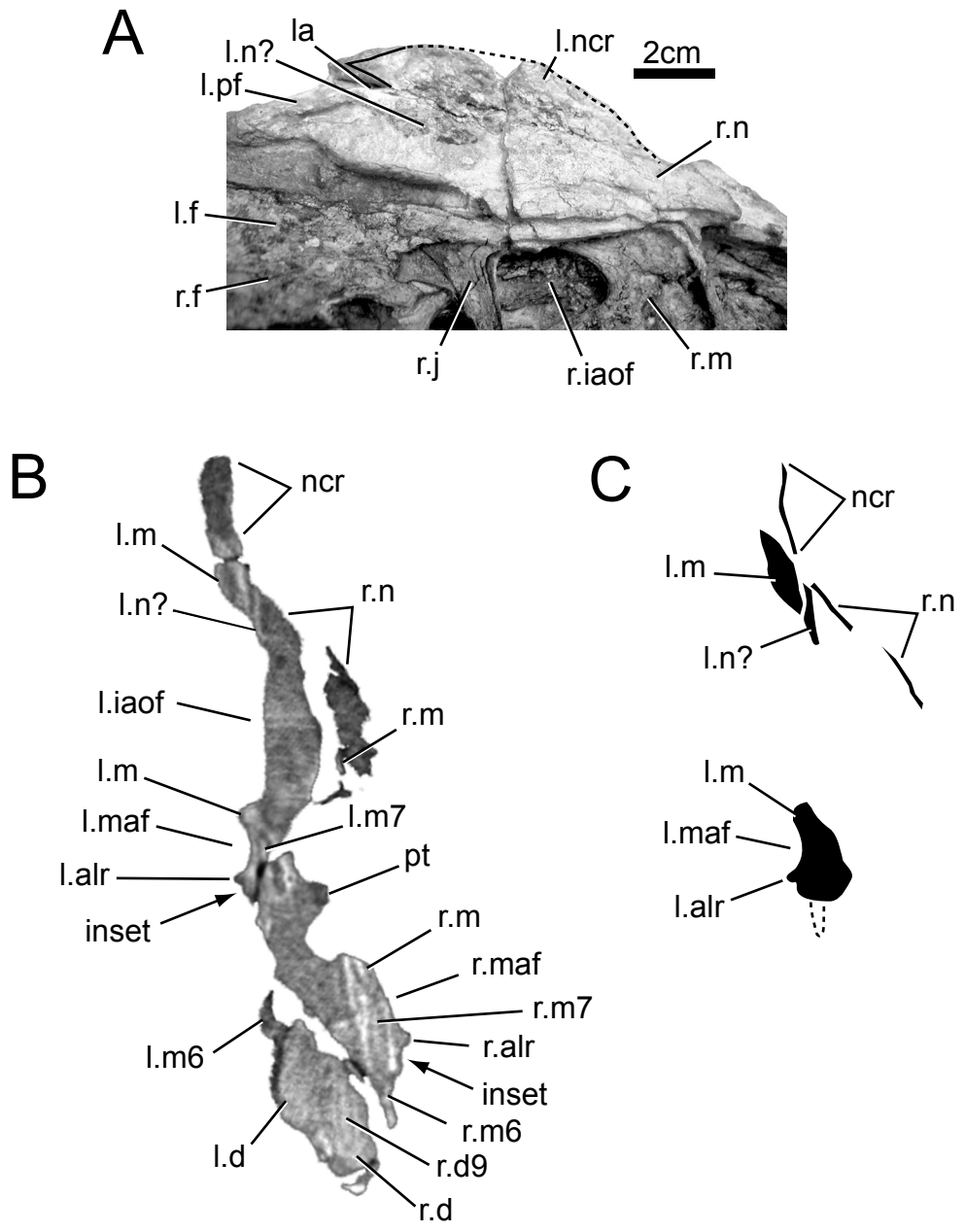


FIGURE 25. Nasal crest of *"Syntarsus" kayentakatae*. A, MNA V2623 skull, close up of nasal crest and dorsal skull elements in right lateral view (looking at dorsomedial surface of nasal crest). B, X-ray CT scan slice through holotype skull (MNA V2623-see Fig. 21D for position and orientation of slice plane) with nasal crest indicated. C, Cross sections of left maxilla, right nasal, nasal crest, and possibly left nasal seen in B.

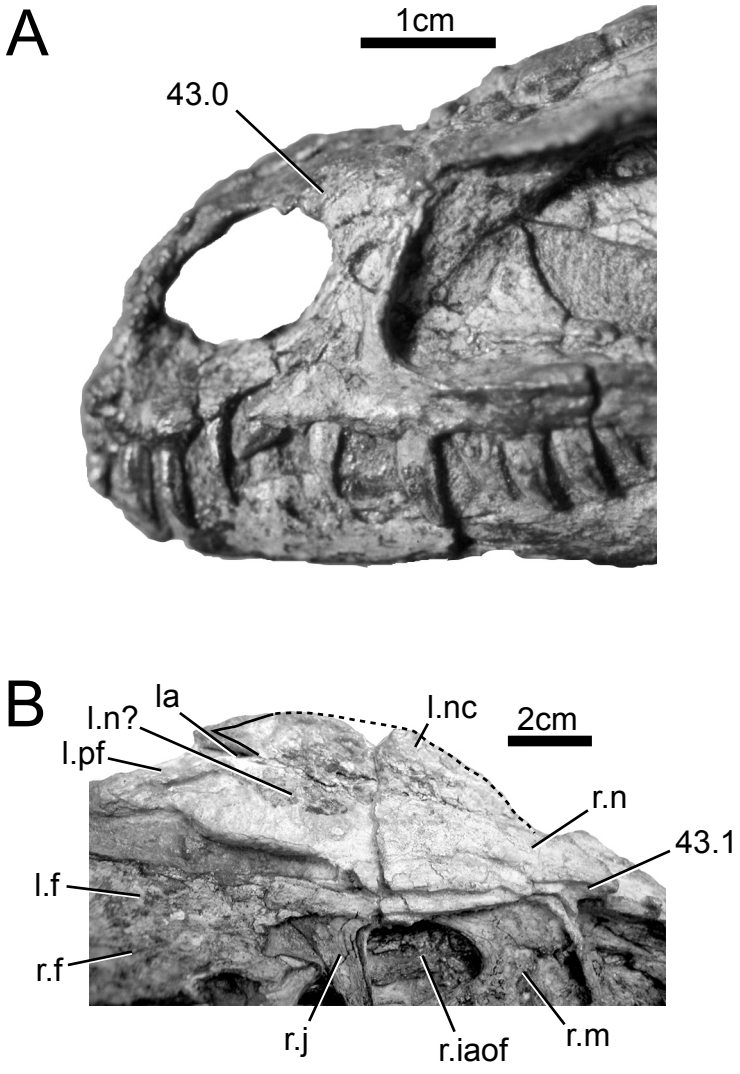


FIGURE 26. Narial fossa. A, *Eoraptor lunensis* (PVSJ 512) rostrum tip in left lateral view, naris lacks lateral concavity and lateral convexity bordering external naris. B, *"Syntarsus" kayentakatae* (MNA V2623) skull in right lateral view, nasal bears lateral concavity bordering external naris.

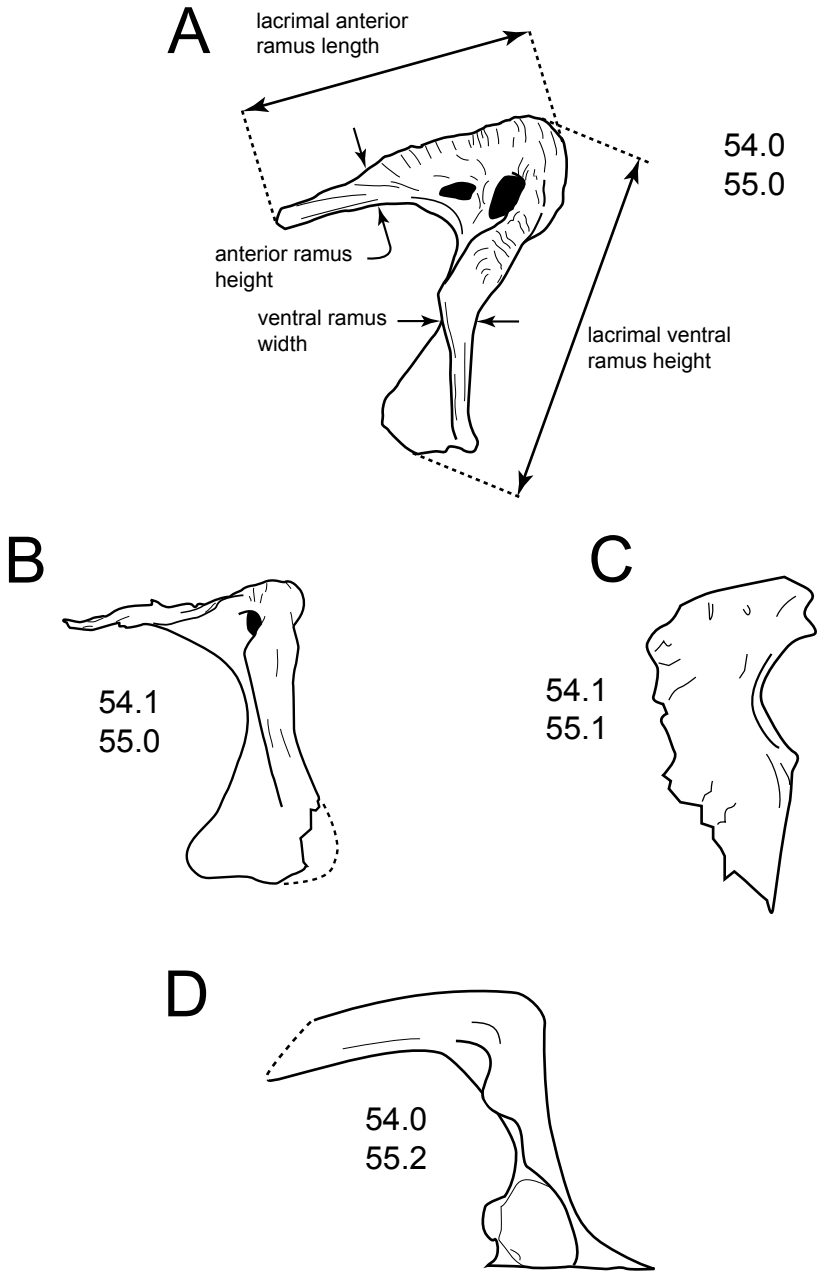


FIGURE 27. Lacrimal anterior ramus proportions. All left lacrimals in lateral view. A, *Allosaurus* (USNM 4734, after Gilmore, 1920) left lacrimal in alteral view. Reference points used to evaluate characters 54 and 55 shown. B, *Torvosaurus* (BYUP 5286, after Britt, 1991). C, *Majungatholus* (based on FMNH PR 2100, Sampson et al., 1998). D, *"Syntarsus" kayentakatae* (MNA V2623). Scoring of characters 54 and 55 given for each. Not to scale.

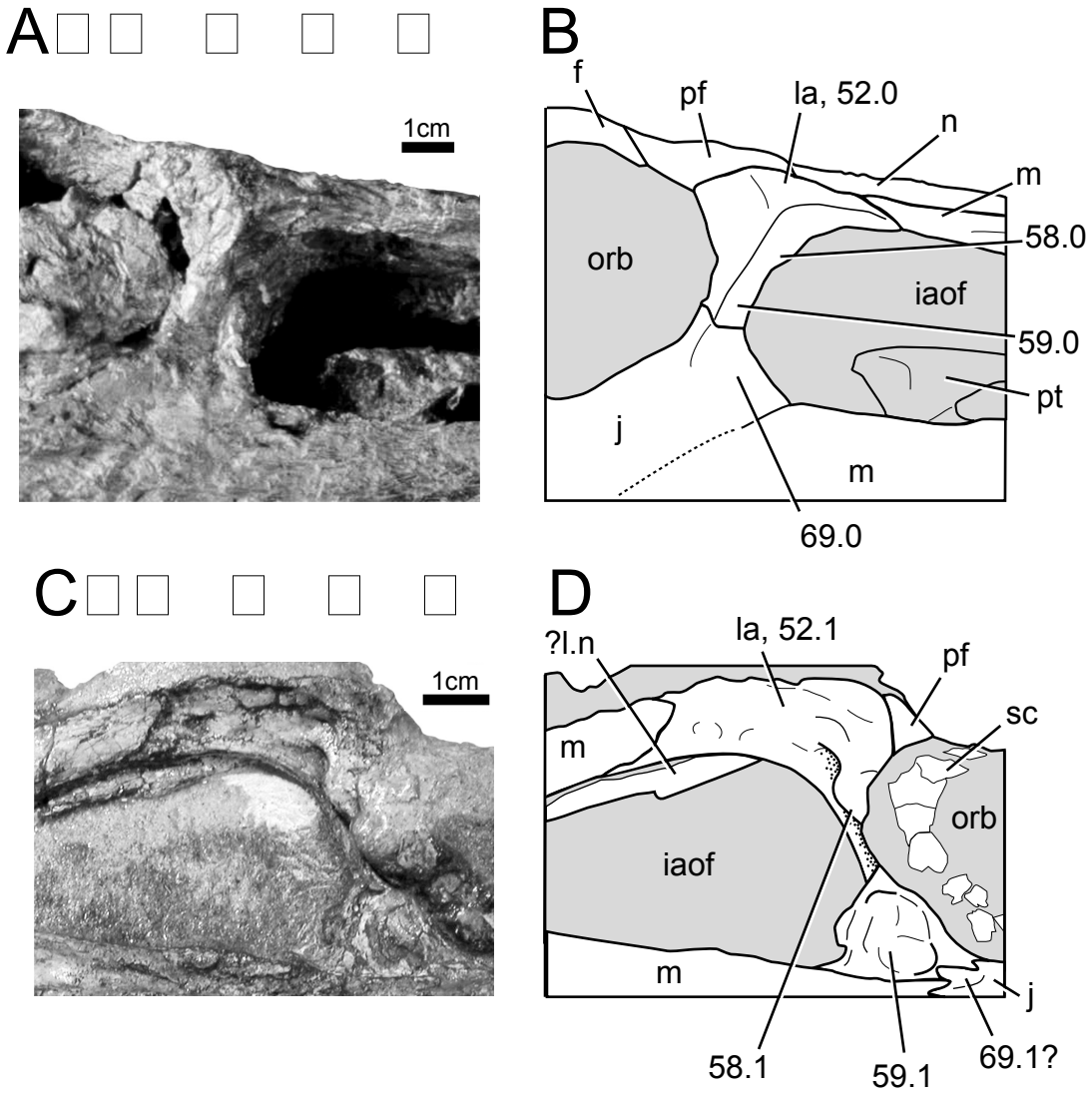


FIGURE 28. Lacrimal antorbital fossa development. A, *Herrerasaurus* (PVSJ 407), right lacrimal and surrounding elements. B, line drawing of A. C, *"Syntarsus" kayentakatae* (MNA V2623) left lacrimal and surrounding elements. D, line drawing of C. Shaded areas represent matrix or major skull openings or matrix.

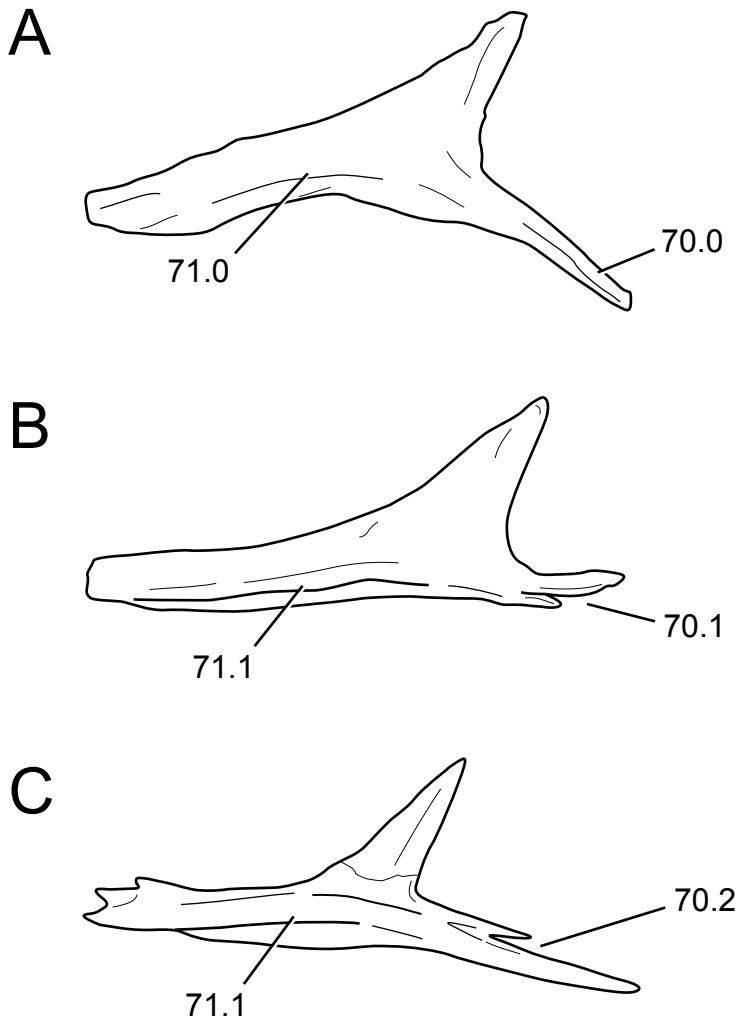


FIGURE 29. Posterior (=quadratojugal) process of jugal. A, *Plateosaurus* (after Galton 1984b; AMNH 6810) left jugal in lateral view. B, *Eoraptor* (PVSJ 512) right jugal (reversed) in lateral view, showing two-pronged posterior process, but ventral prong shorter than dorsal prong. C, *"Syntarsus" kayentakatae* (MNA V2623) left jugal in lateral view demonstrating two-pronged posterior process with much longer ventral prong. Not to scale.

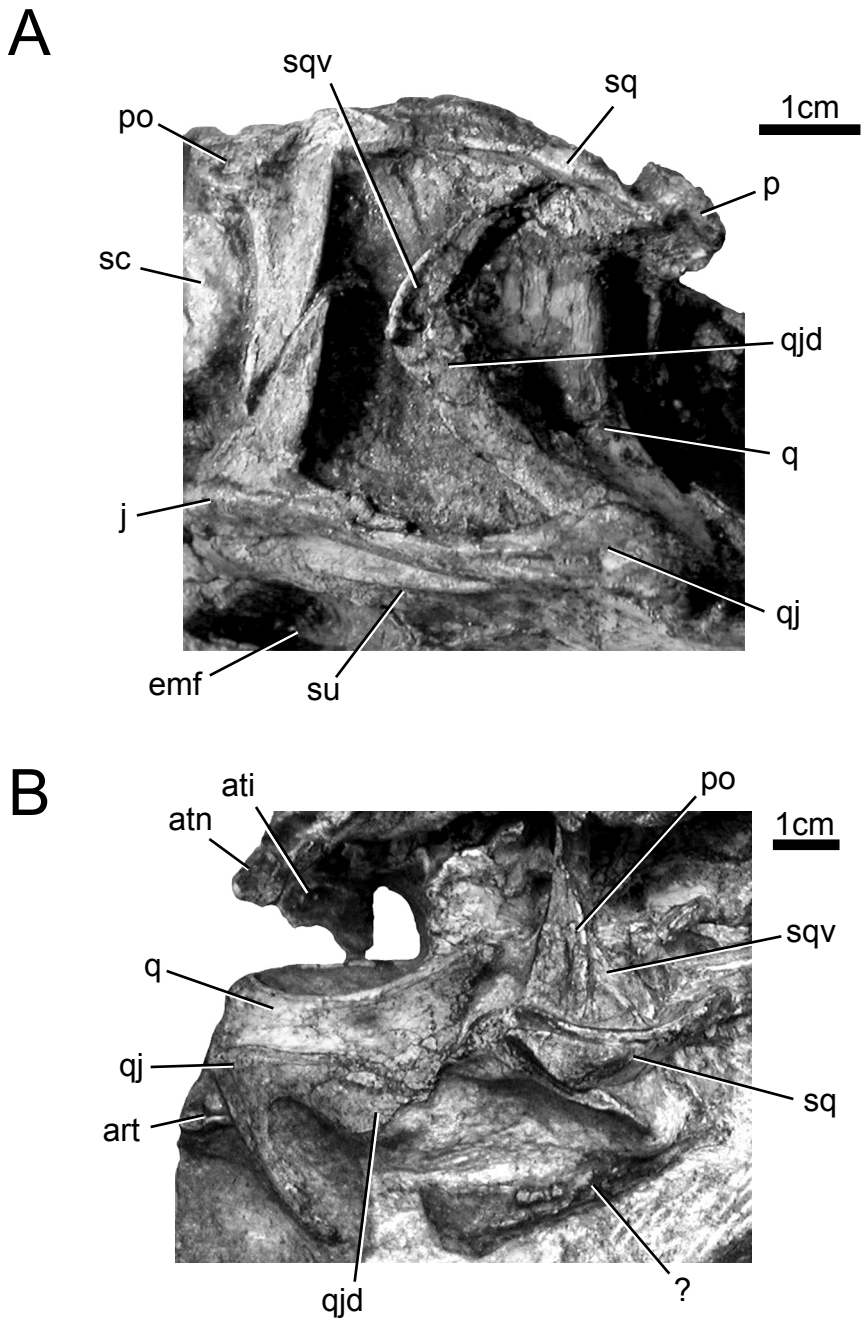


FIGURE 30. Squamosal-quadratojugal contact in *"Syntarsus" kayentakatae*. A, left infratemporal region of MNA V2623 in lateral view. Note dorsoventral crushing of elements. B, disarticulated right suspensorium elements as preserved in MNA V2623. Looking at posterior surface of quadrate, posterolateral surface of quadratojugal, dorsal to right. Postorbital and squamosal in lateral view, anterior to left and ventral to top of image.

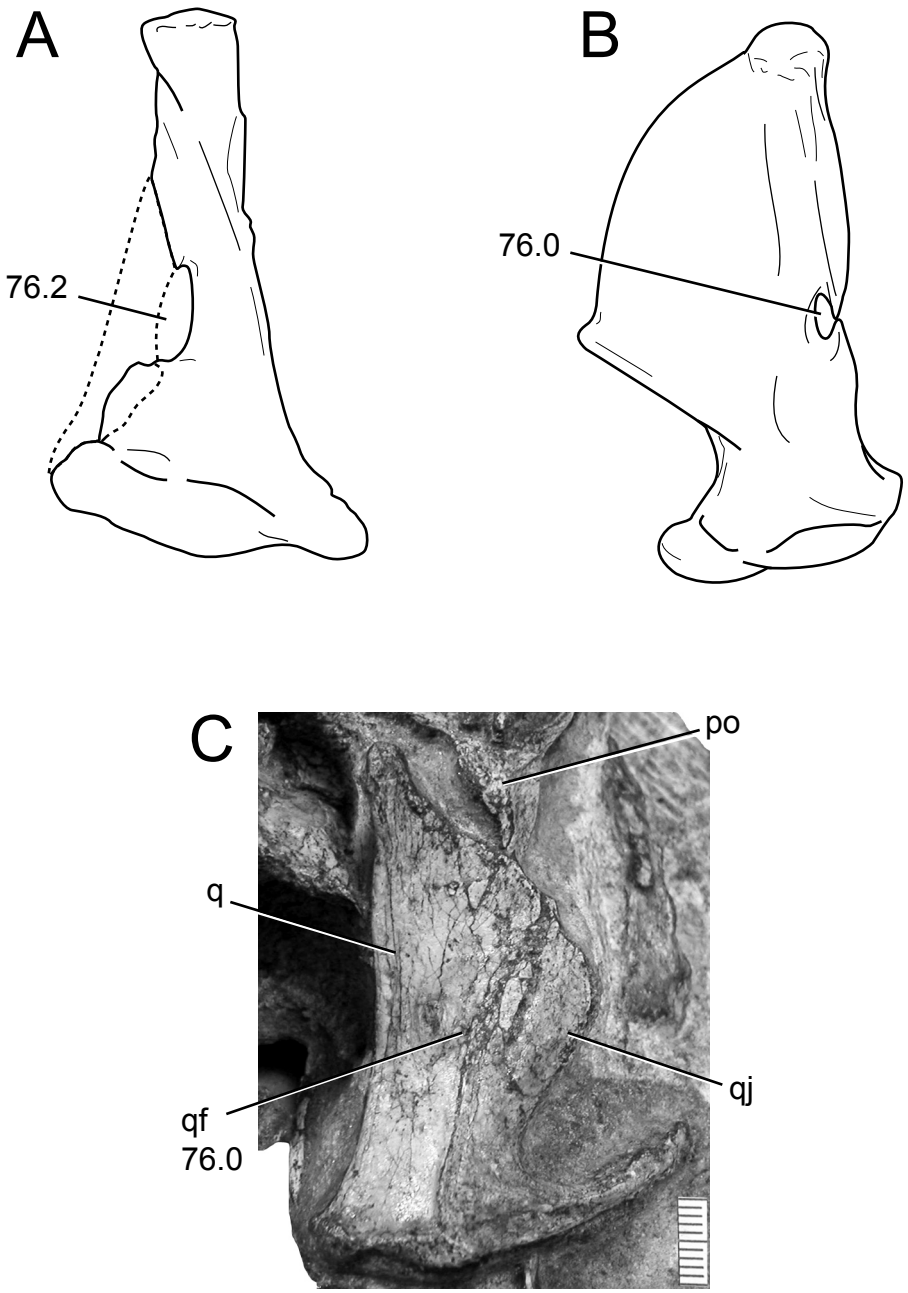


FIGURE 31. Quadrate foramen relative size and position. A, *Baryonyx* (BMNH R9951) left qudarate, posterior view. Quadratojugal reconstructed with dashed lines (after Charig and Milner, 1997). B, *Allosaurus* left quadrate in anterior view (after Madsen, 1976). C. *"Syntarsus" kayentakatae* (MNA V2623) right quadrate and quadratojugal, posterior view. Scale bar in C equals 1cm.

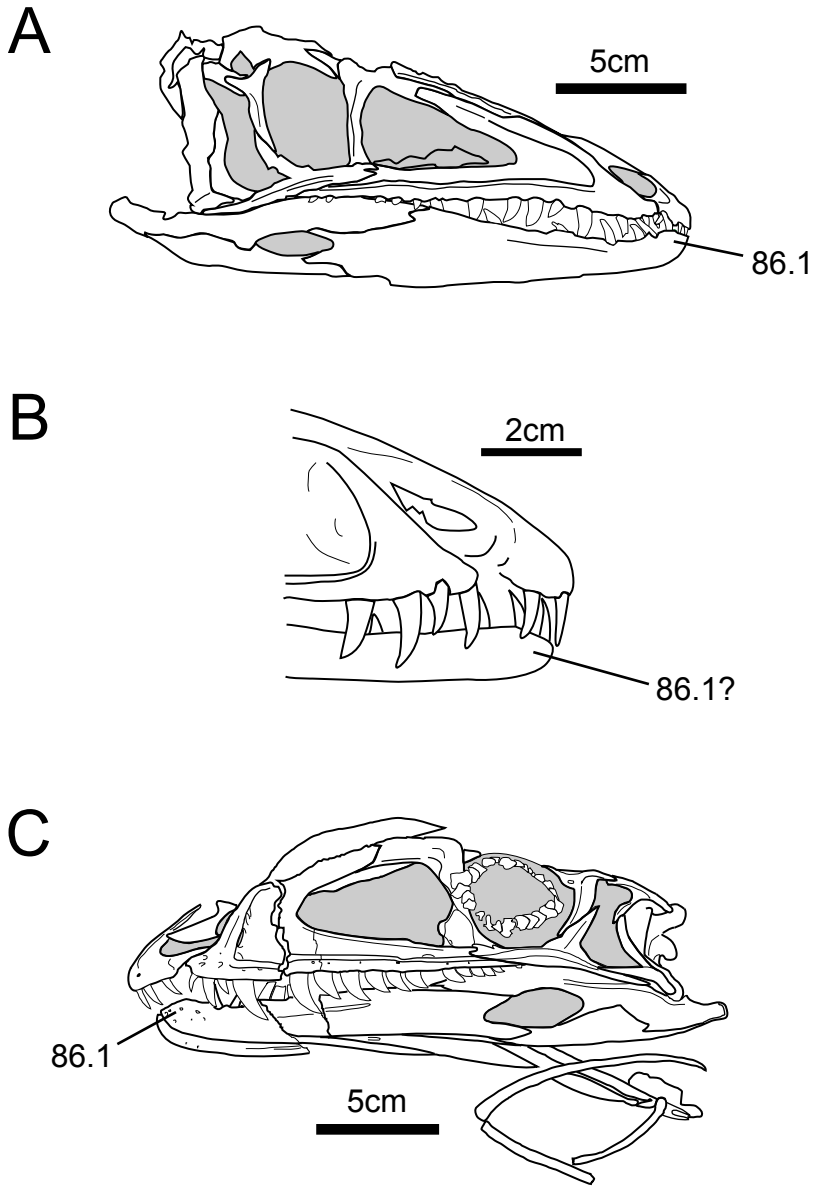


FIGURE 32. Raised anterior tip of dentary. A, *Coelophysis* (AMNH 7224) skull in right lateral view (after Colbert, 1989). B, *Coelophysis* (MCZ 4327), tip of rostrum in right lateral view (after Colbert, 1989). Borders of external naris and maxillary process of right premaxilla indistinct. C, *"Syntarsus" kayentakatae* (MNA V2623) skull in left lateral view (after Tykoski and Rowe, 2004).

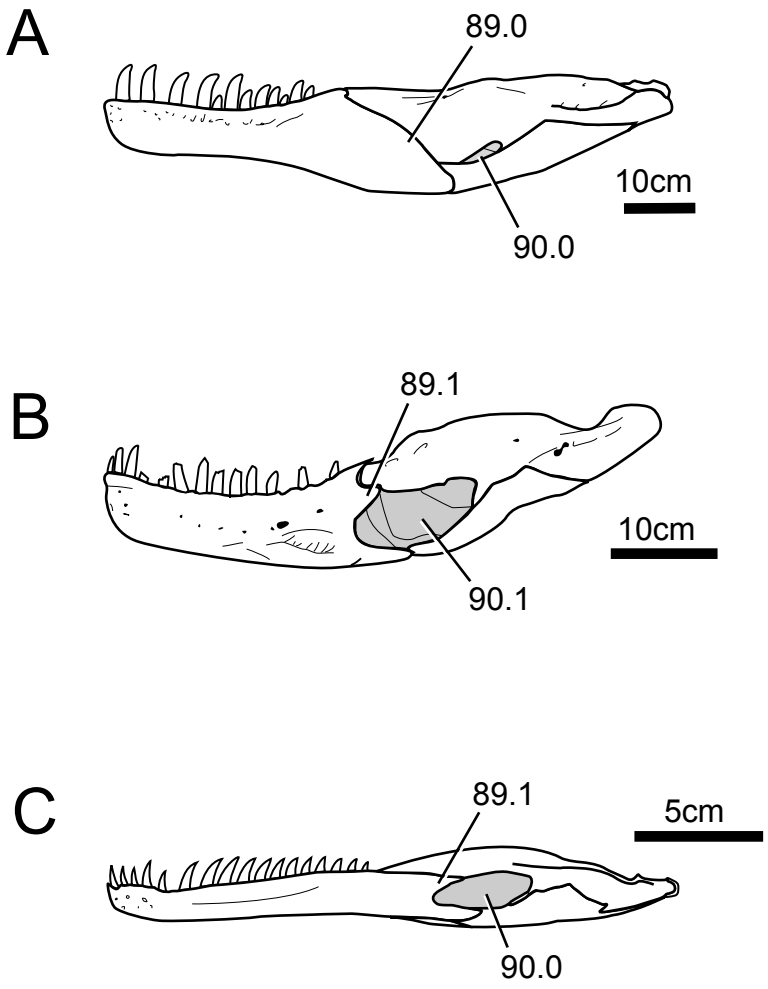


FIGURE 33. Posterior processes of dentary. A, *Allosaurus* (after Madsen, 1976) reconstruction of left mandible, lateral view. B, *Carnotaurus* (MACN-CH 894) left mandible, lateral view (after Bonaparte et al., 1990). C, *"Syntarsus" kayentakatae* (based on MNA V2623), reconstruction of left mandible, lateral view.

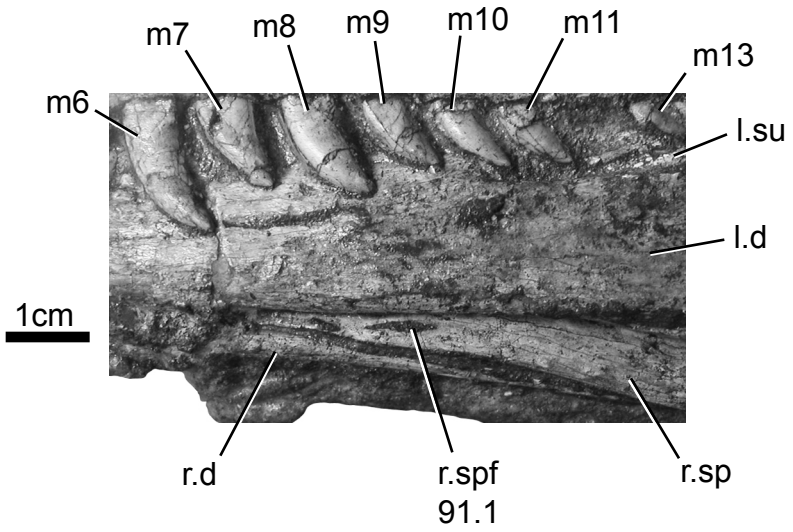


FIGURE 34. Splenial foramen. *"Syntarsus" kayentakatae* right splenial in medial view, as viewed from left lateral side of holotype skull (MNA V2623). Splenial foramen filled with hematitic sediment, but clearly visible in right splenial.

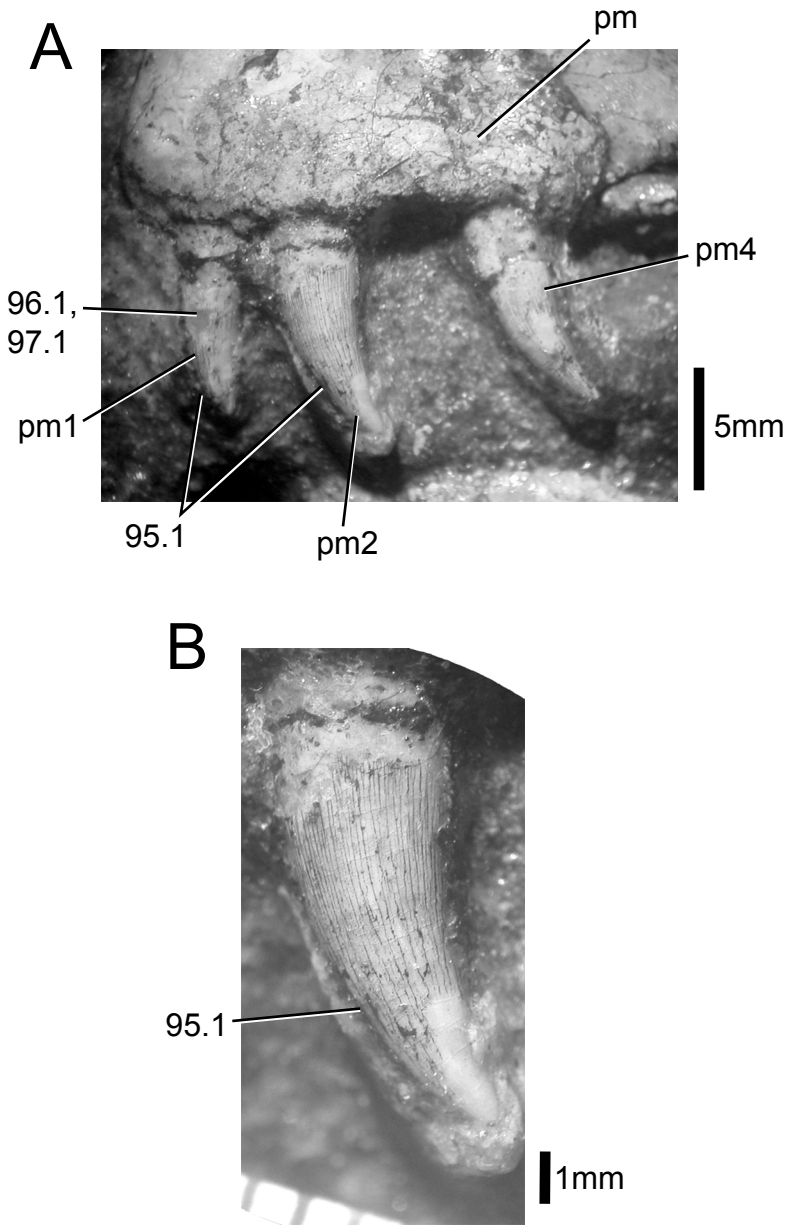


FIGURE 35. Premaxillary teeth of *"Syntarsus" kayentakatae* (MNA V2623). A, first, second, fourth premaxillary teeth, left side in lateral view. Note nearly straight axis of first tooth. B, close-up of second premaxillary tooth showing lack of serrations along mesial and distal edges of tooth.

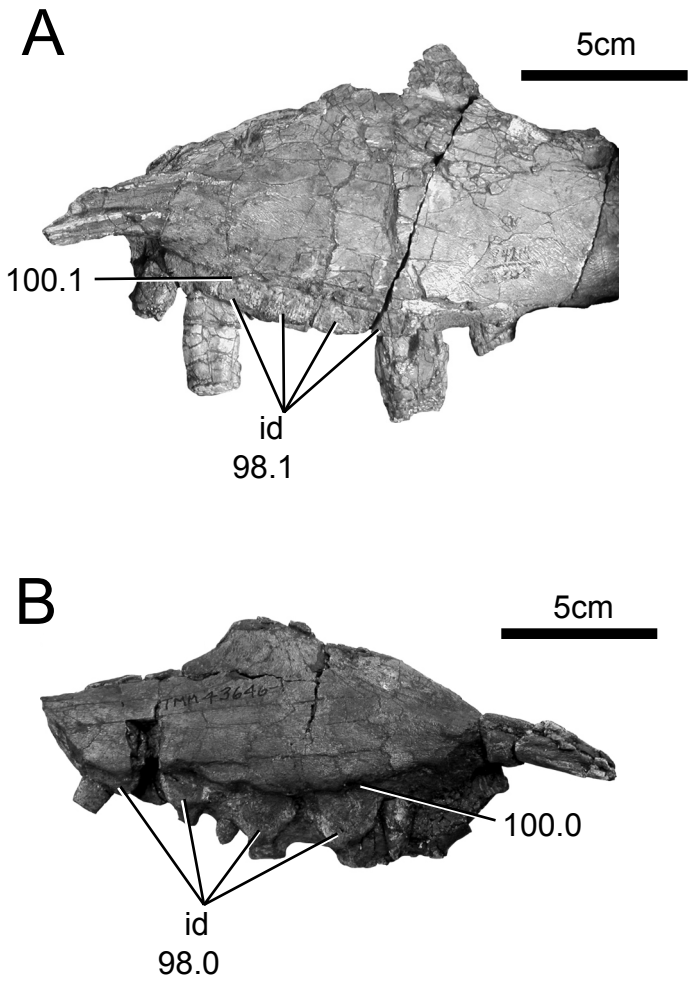


FIGURE 36. Interdental plates in *Dilophosaurus.* A, UCMP 37303 anterior part of right maxilla in medial view with fused and partially obscured interdental plates. B, TMM 43646-1, partial left maxilla in medial view with separate and broadly exposed interdental plates.

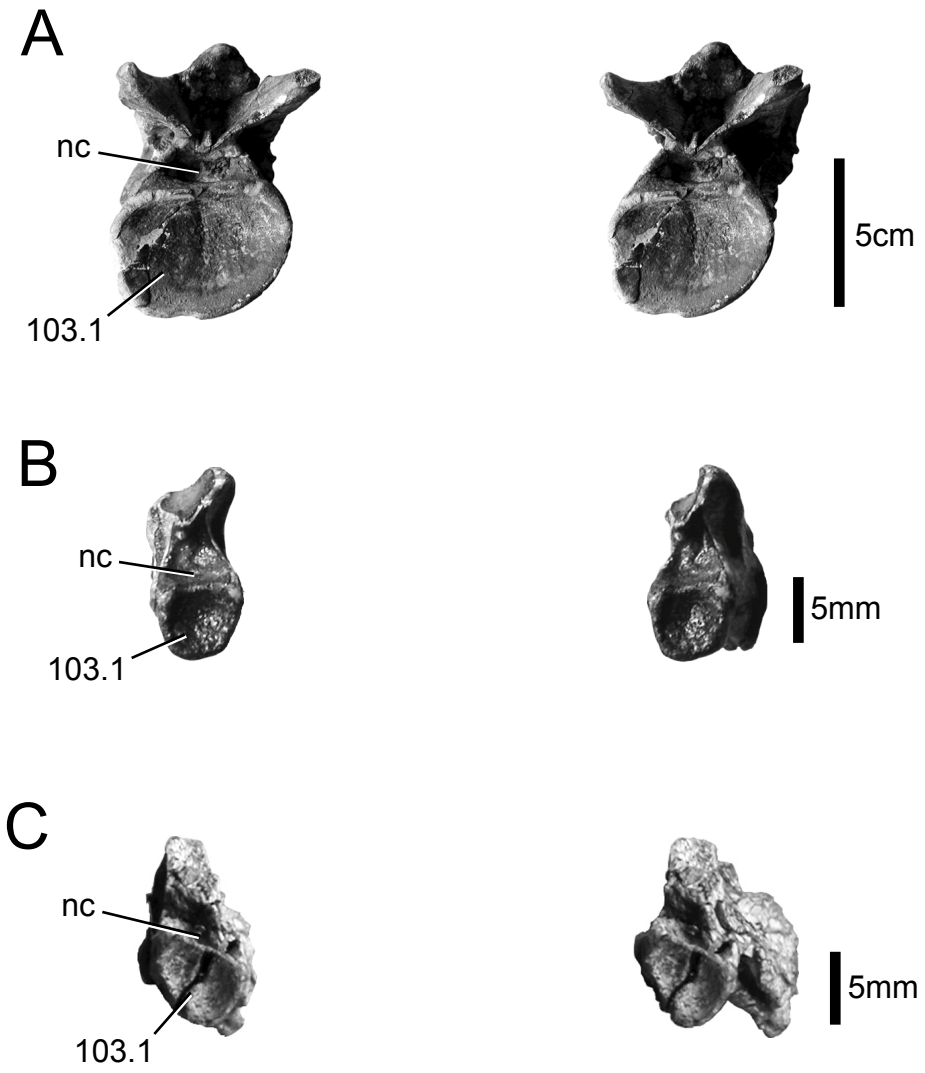


FIGURE 37. Deeply concave posterior surfaces in coelophysoid cervical centra. Stereophotopairs. A, *Dilophosaurus* (TMM 43646-3), fourth? cervical vertebra. B, Shake-N-Bake taxon (TMM 43689-23), mid-cervical vertebra. C, *Coelophysis* (TMM 45559-13) cervical vertebra of small individual. All in posterior view.

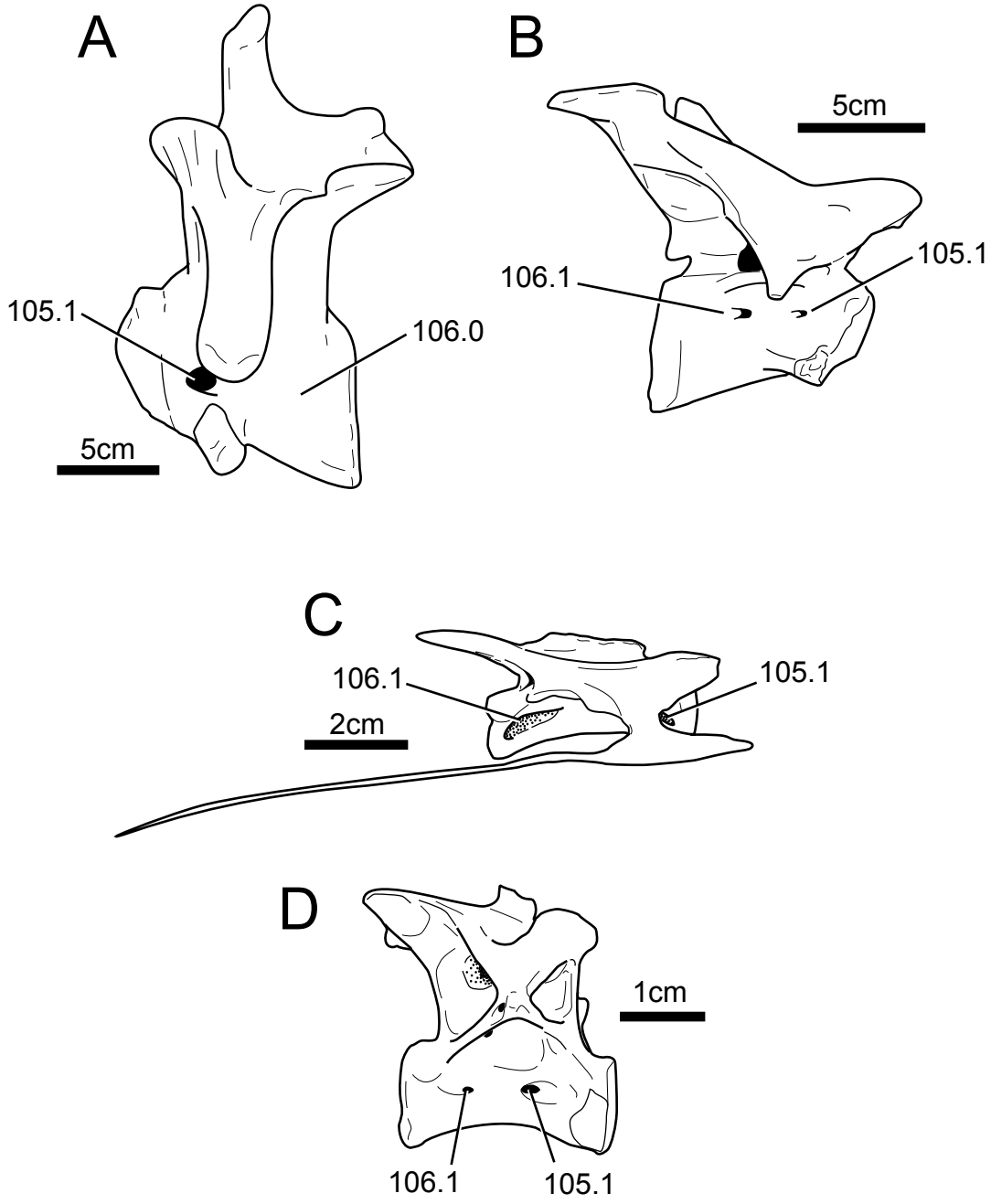


FIGURE 38. Number and location of cervical pleurocoels. A, *Allosaurus* ninth cervical vertebra, left lateral view (after Madsen, 1976). B, *Carnotaurus* (MACN-CH 894) third cervical vertebra, right lateral view (after Bonaparte et al., 1990). C, *"Syntarsus" kayentakatae* (MNA V2623) seventh cervical vertebra and rib, right lateral view. D, *Masiakasaurus* (FMNH PR 2141) posterior cervical vertebra, right lateral view (after Carrano et al., 2002).

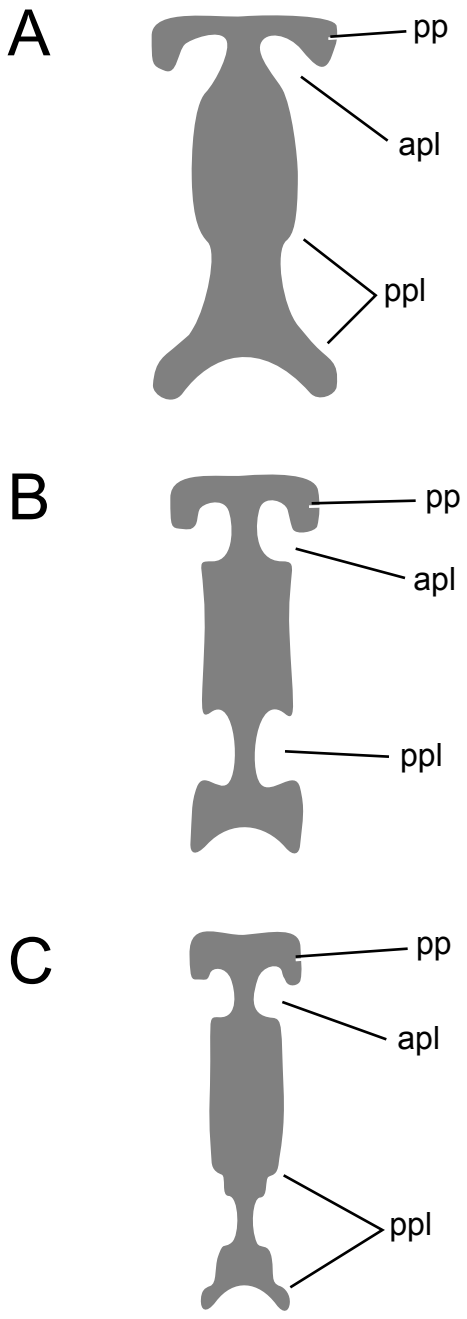


FIGURE 39. Horizontal sections of stylized coelophysoid cervical centra. Illustrates different forms of cervical pleurocoel expression . A, *Dilophosaurus*, based upon UCMP 37302. B, *"Syntarsus" kayentakatae,* based upon MNA V2623. C, Shake-N-Bake taxon, composite based upon several partial to complete cervical vertebrae. Not to scale.

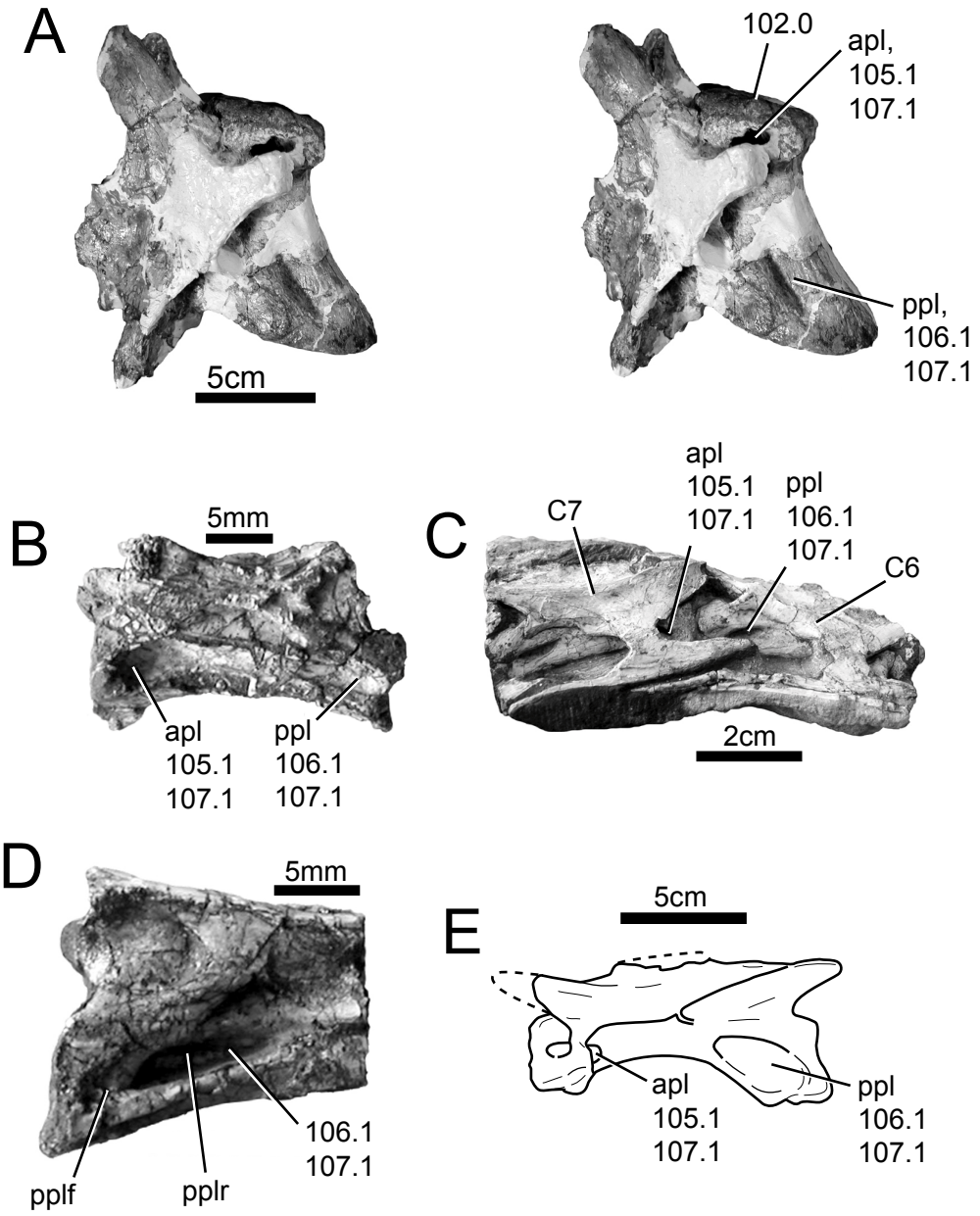


FIGURE 40. Cervical pleurocoels in coelophysoids and *Elaphrosaurus*. A, *Dilophosaurus* (UCMP 37302) stereophoto of sixth cervical vertebra, right lateral view. B, *Coelophysis* (TMM 45559-13), mid-cervical vertebra, left lateral view. C, *"Syntarsus" kayentakatae* (MNA V2623) sixth and seventh cervical vertebrae in right lateral view. D, Shake-N-Bake taxon (TMM 43689-20) posterior half of mid-cervical vertebra, right lateral view. E, *Elaphrosaurus* seventh cervical vertebra in left lateral view (after Janensch, 1925).

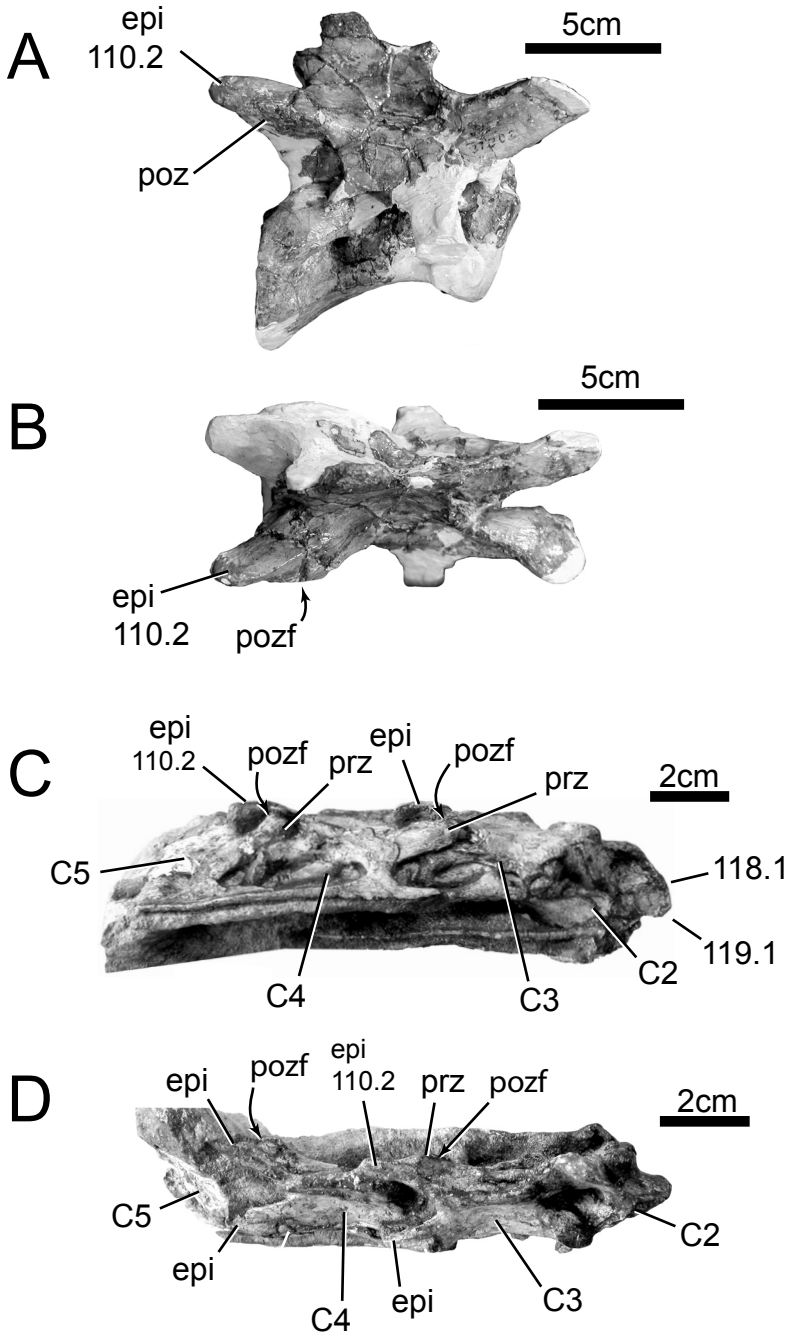


FIGURE 41. Coelophysoid cervical epipophyses. Epipophyses project posterolaterally beyond the postzygapophyses. A, *Dilophosaurus* (UCMP 37302) fourth cervical vertebra, right lateral view. B, same as A, dorsal view. C, *"Syntarsus" kayentakatae* (MNA V2623) second through fifth cervical vertebrae, right lateral view. D, same as C, dorsal view.

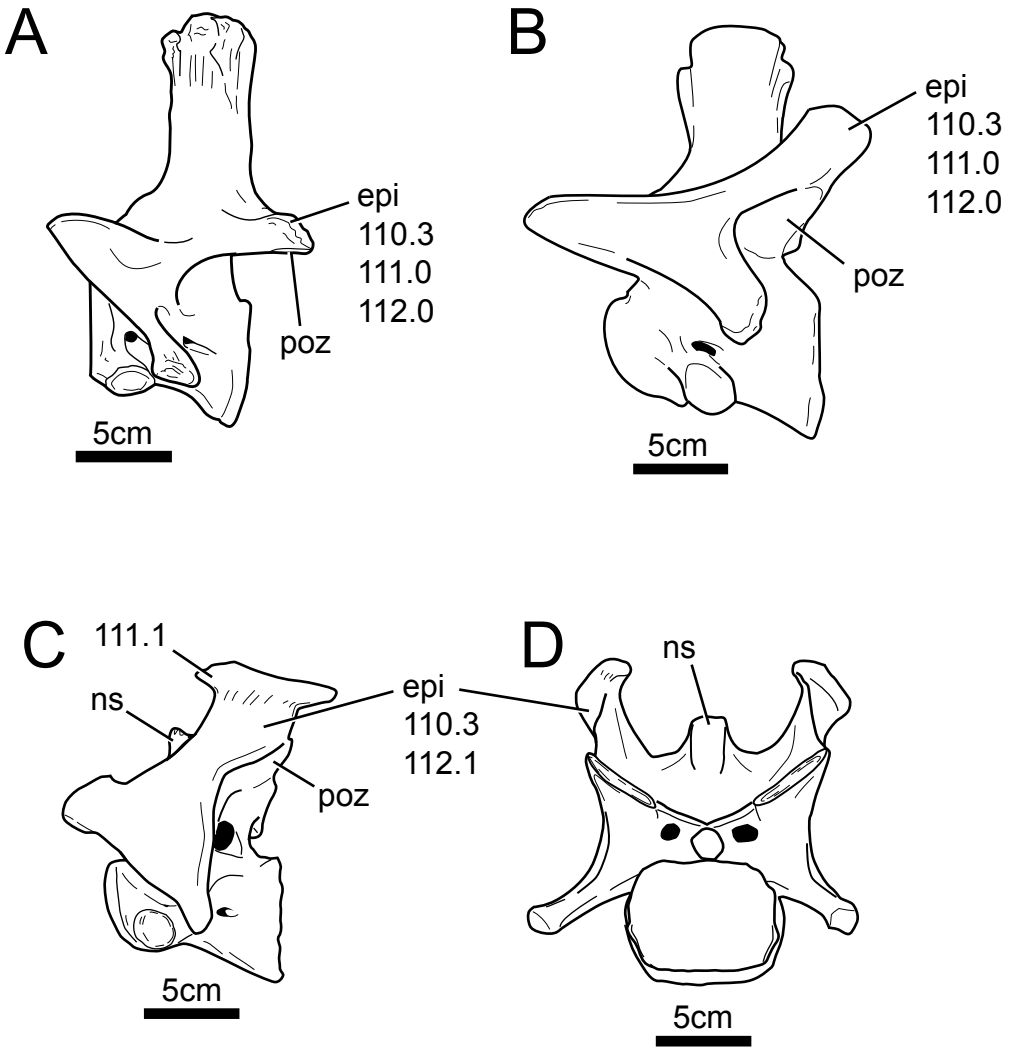


FIGURE 42. Cervical epipophysis size and morphology. A, *Ceratosaurus* (USNM 4735) sixth cervical vertebra, left lateral view (after Gilmore, 1920). B, *Allosaurus* fifth cervical vertebra, left lateral view (after Madsen, 1976). C, *Carnotaurus* (MACN-CH 894) sixth cervical vertebra, left lateral view (after Bonaparte, 1990). D, same as in C, anterior view.

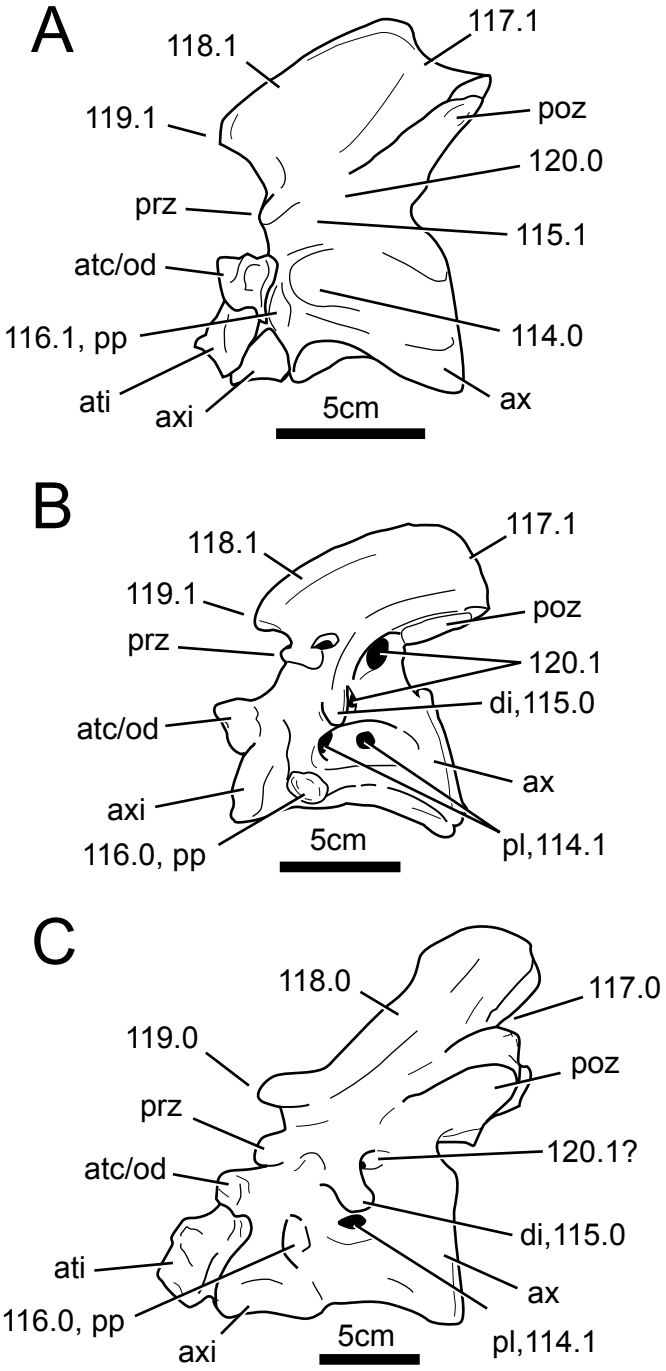


FIGURE 43. Theropod atlas-axis complex. Several characters highlighted in figure. A, *Dilophosaurus* (UCMP 37302). B, *Ceratosaurus* (after Gilmore, 1920). C, *Allosaurus* (after Madsen, 1976). All in left lateral view.

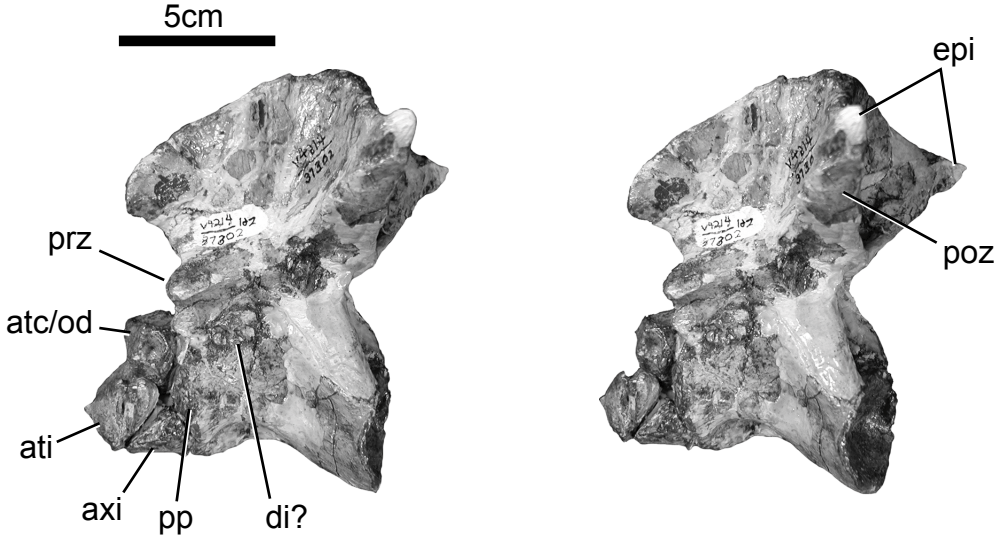


FIGURE 44. *Dilophosaurus* atlas-axis complex. Stereophotopair of type specimen (UCMP 37302), left lateral view. For character state coding of characters 114-120, see Figure 43A.

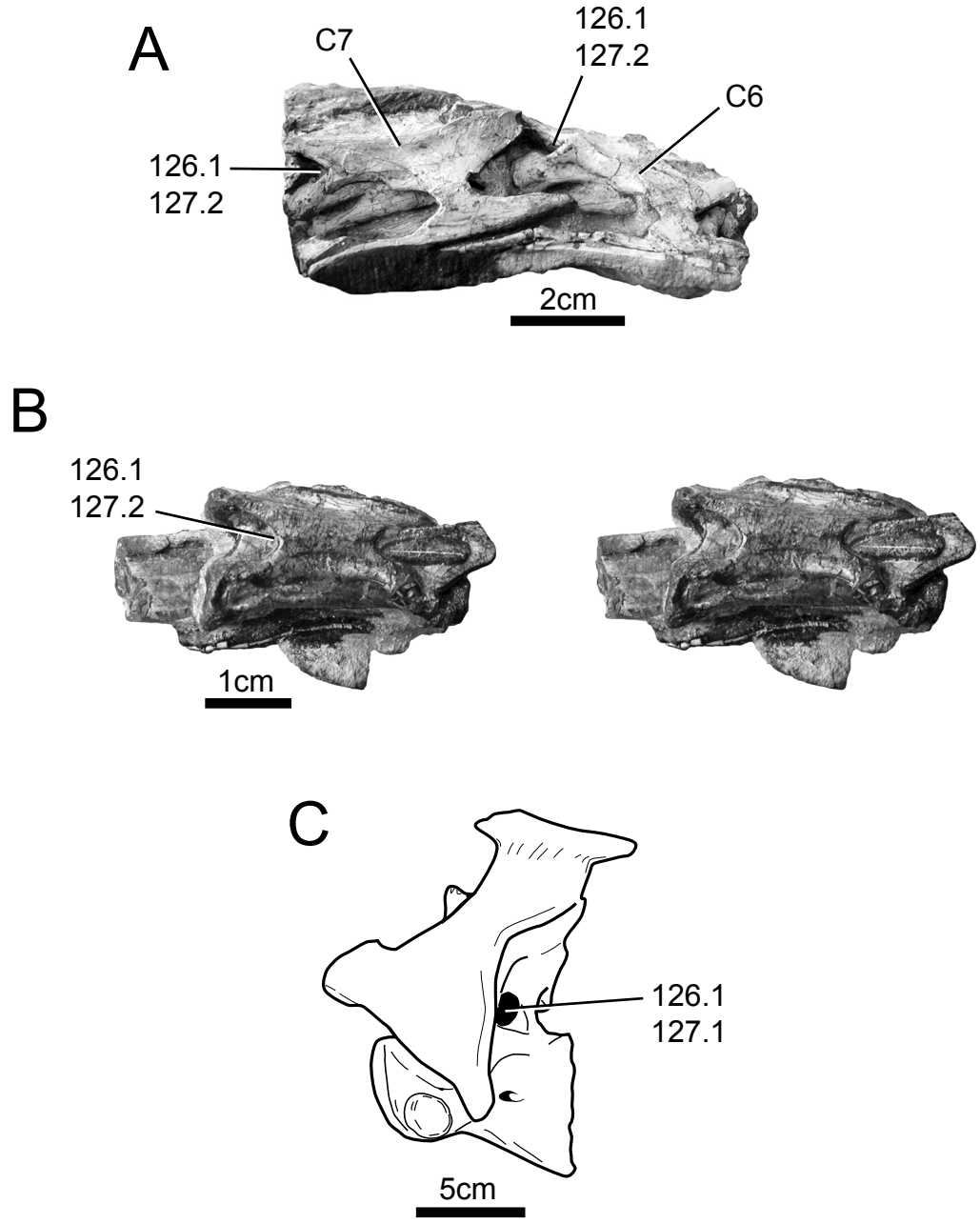


FIGURE 45. Cervical neural arch cavities and openings. A, *"Syntarsus" kayentakatae* (MNA V2623), sixth and seventh cervical vertebrae, right lateral view. B, Shake-N-Bake taxon (TMM 43689-18), stereophotopair of mid-cervical vertebra, right lateral view. C, *Carnotaurus* (MACN-CH 894) sixth cervical vertebra in left lateral view (after Bonaparte, et al., 1990).

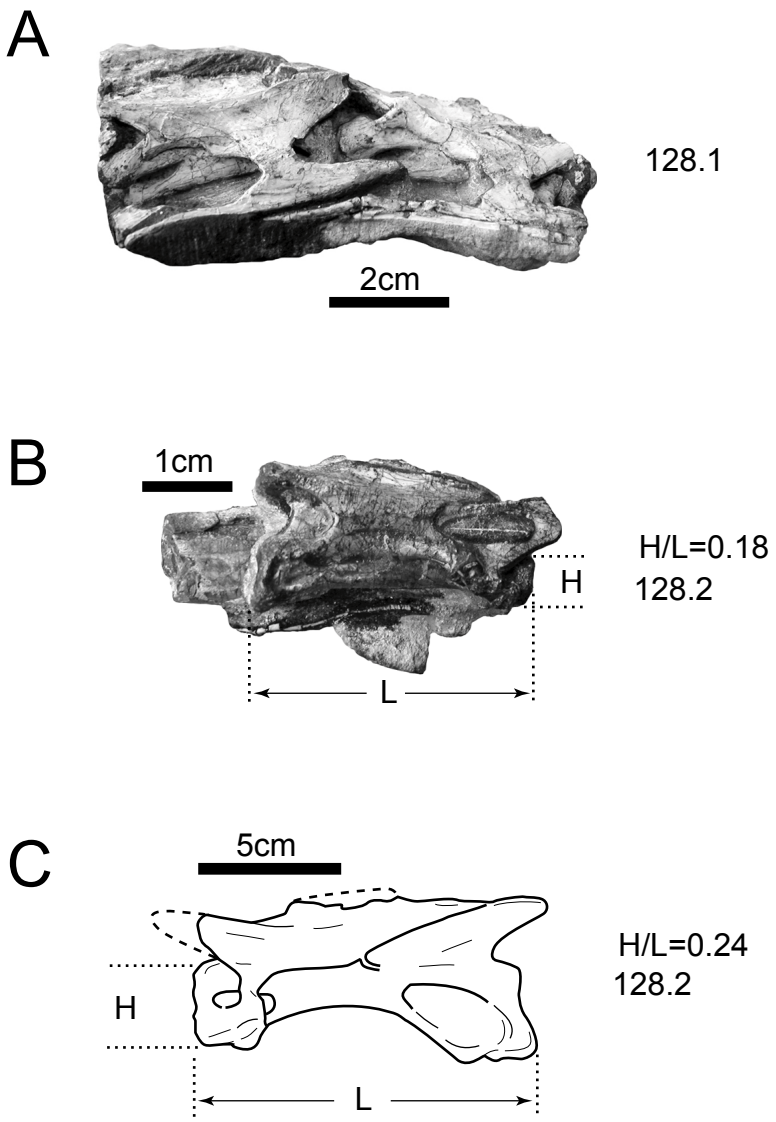


FIGURE 46. Cervical centrum elongation in coelophysoids and *Elaphrosaurus*. A, *"Syntarsus" kayentakatae* (MNA V2623) sxith and seventh cervical vertebrae in right lateral view. Anterior faces of centra are obscured but best measurements suggest centra are between three and four times longer than anterior face is high. B, Shake-N-Bake taxon (TMM 43689-18) mid-cervical in right lateral view. C, *Elaphrosaurus* seventh cervical in left lateral view (after Janensch, 1925).

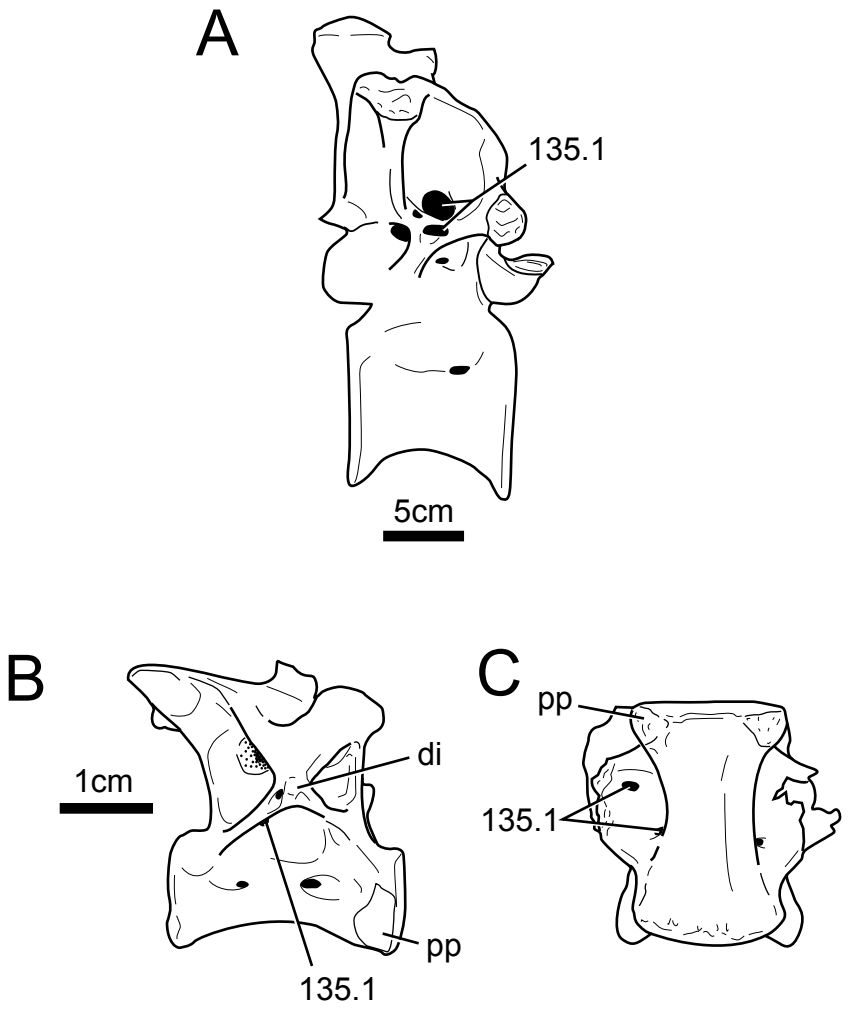


FIGURE 47. Accessory neural arch foramina in abelisauroids. A, *Carnotaurus* (MACN-CH 894) eigth dorsal vertebra in right lateral view (after Bonaparte et al., 1990). B and C, *Masiakasaurus* posterior cervical vertebra (FMNH PR 2141) in B, right lateral, and C, ventral views (after Carrano et al, 2002).

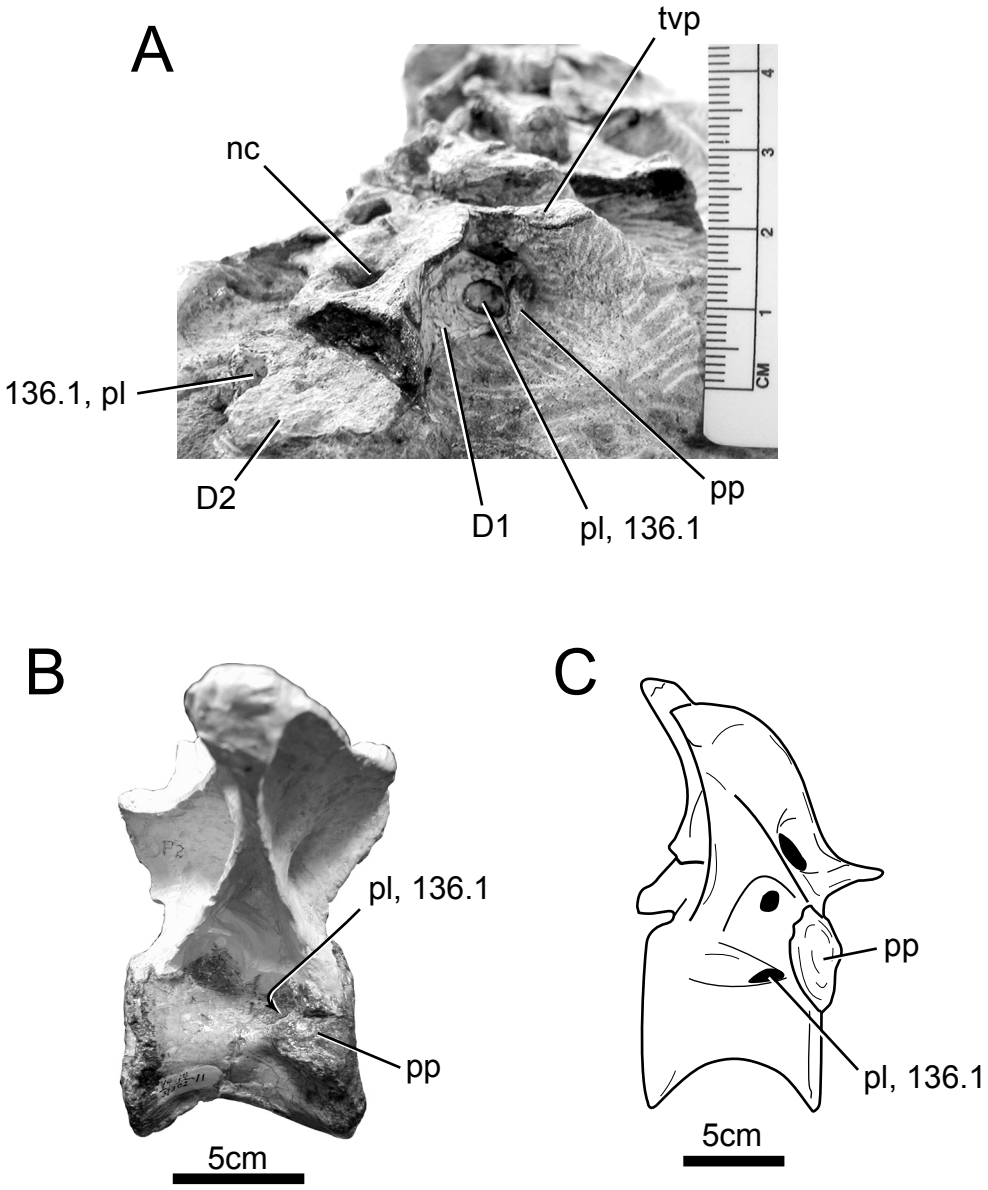


FIGURE 48. Pleurocoels in the anterior dorsal vertebrae. A, *"Syntarsus" kayentakatae* (MNA V2623), block containing several vertebrae. First dorsal vertebra (V11) in right posterolateral view. B, *Dilophosaurus* (UCMP 37302) first dorsal (second pectoral of Welles, 1984) vertebra (V11) in right lateral view. Entire neural arch is reconstructed in plaster. C, *Carnotaurus* (MACN-CH 894) fourth dorsal (V14) in right lateral view (after Bonaparte et al., 1990).

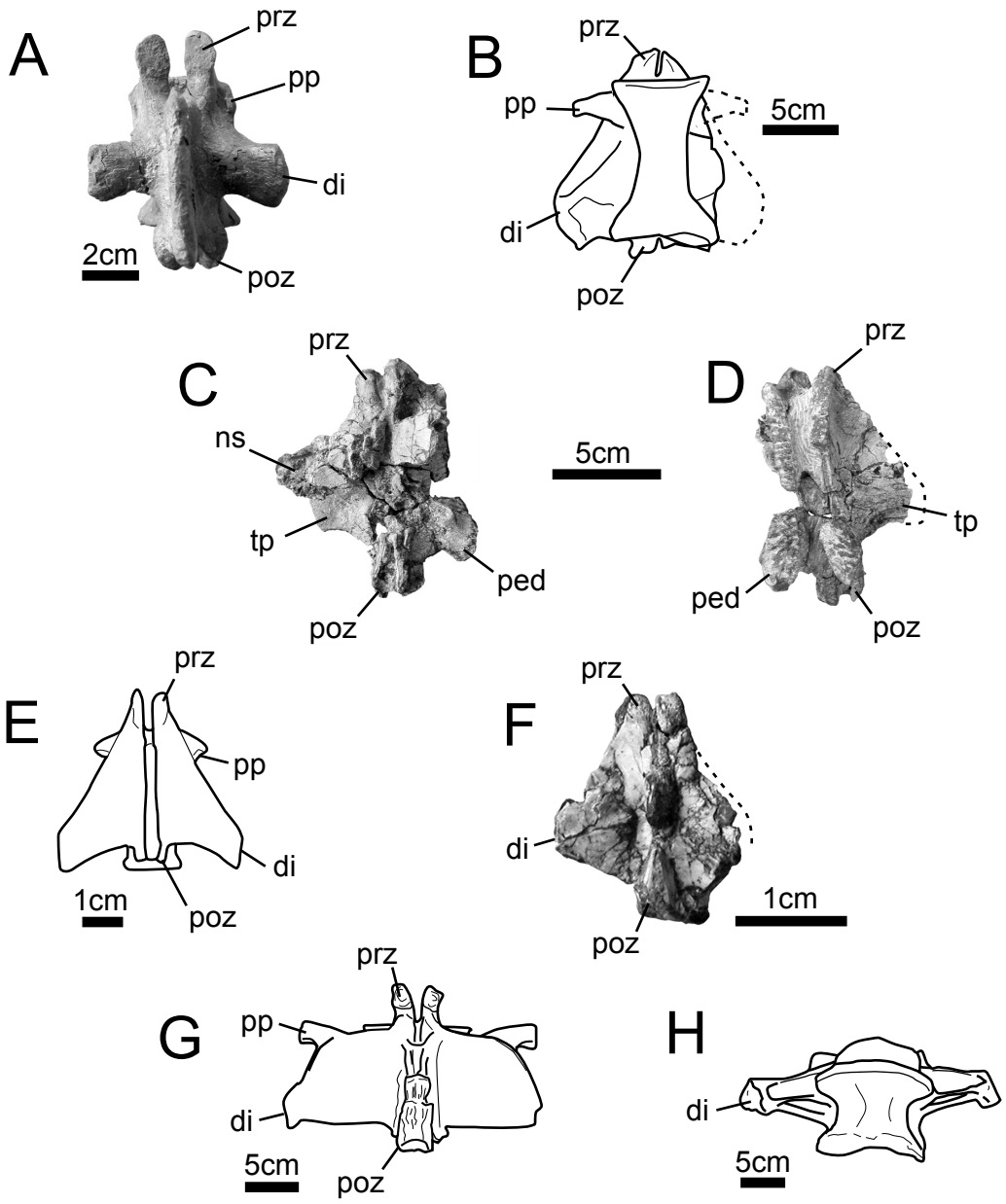


FIGURE 49. Dorsal vertebral transverse processes. A, prosauropod (TMM 42179-20), dorsal view. B, *Ceratosaurus* (BYUVP 4952) ventral view, (after Britt, 1991). C, *Dilophosaurus* (TMM 43646-62) neural arch, dorsal view. D, *Dilophosaurus* (TMM 43646-62) neural arch, ventral view. E, *Syntarsus rhodesiensis*, dorsal view (after Raath, 1977). F, Shake-N-Bake taxon (MCZ 9457) anterior dorsal, dorsal view. G, *Carnotaurus* (MACN-CH 894) 8th dorsal, dorsal view (after Bonaparte et al., 1990). H, *Torvosaurus* (BYUVP 4998), 4th dorsal, ventral view (after Britt, 1991).

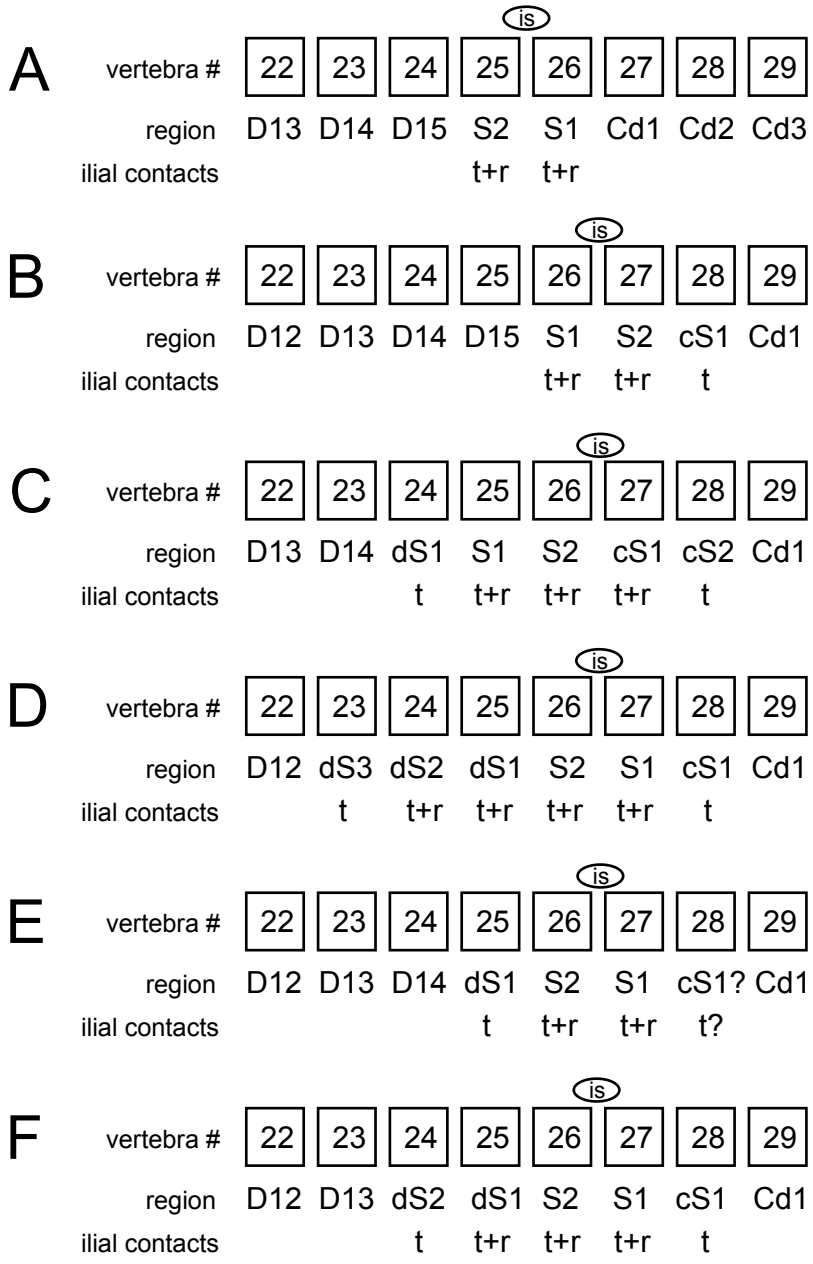


FIGURE 50. Diagrams of saurischian sacral homology. A, hypothesized ornithodire or *Herrerasaurus* (Bonaparte, 1975; Novas, 1993). B, *Plateosaurus* (Galton, 1990). C, *Allosaurus* and most other theropods *sensu* Madsen (1976), Molnar et al., (1990), Sereno (1999a), Carrano et al., (2002)-state 1; Tykoski and Rowe (2004). D, ceratosauroid basal condition (after Carrano et al., 2002-state 2). E, *Eoraptor* (pers. obs. cast PVSJ-512). F, revised hypothesis of sacral homology in coelophysoids, *Allosaurus*, and other tetanurans. r=rib contact with ilium, t=transverse process contact with ilium, is=ischial peduncle of ilium position relative to vertebral series.

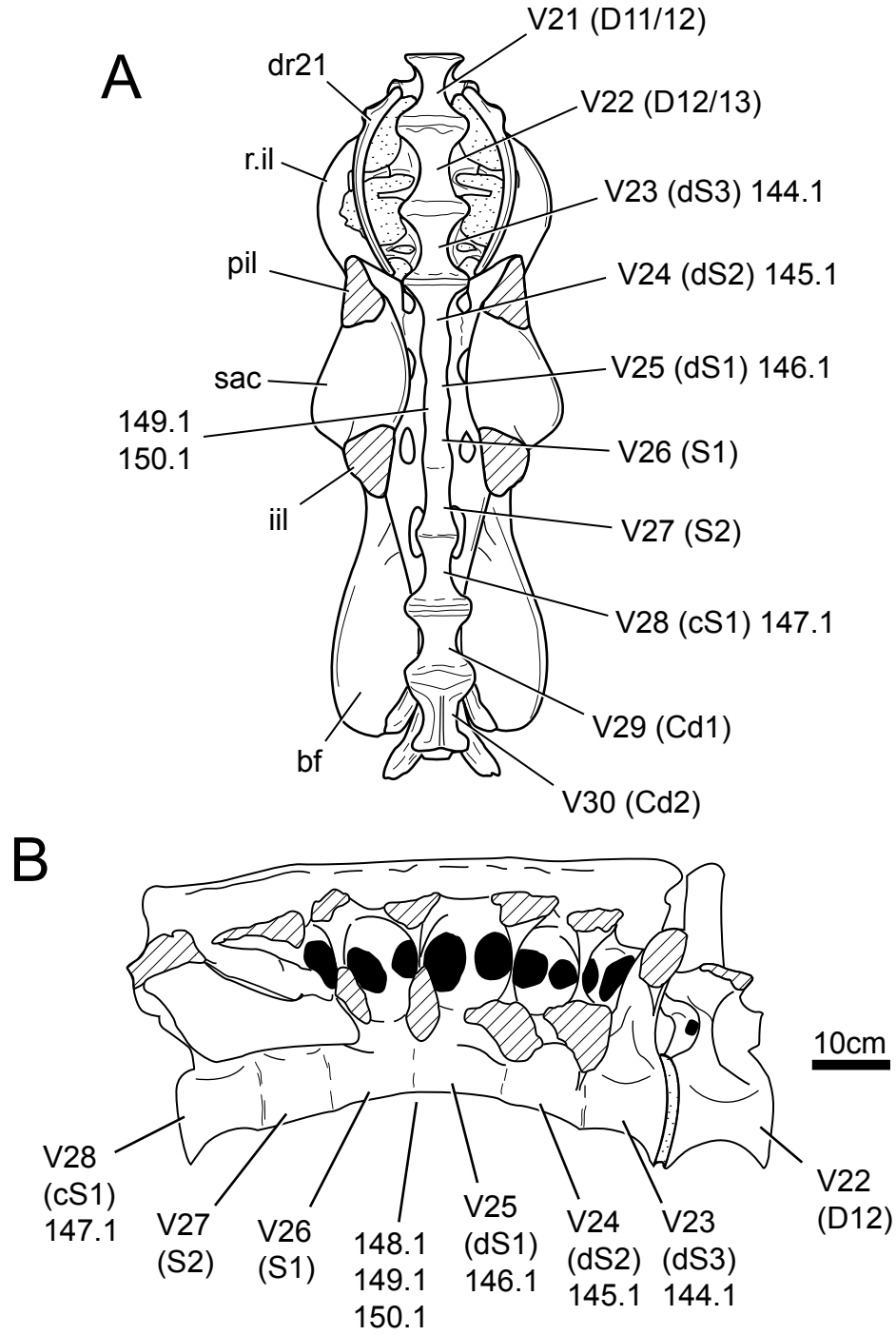


FIGURE 51. Ceratosauroid sacra. A, *Ceratosaurus* (USNM 4735) synsacrum, ventral view (after Gilmore, 1920). B, *Carnotaurus* (MACN-CH 894) sacrum, right lateral view (after Bonaparte et al., 1990). Cross-hatching=sectioned bone. Black fill= foramen

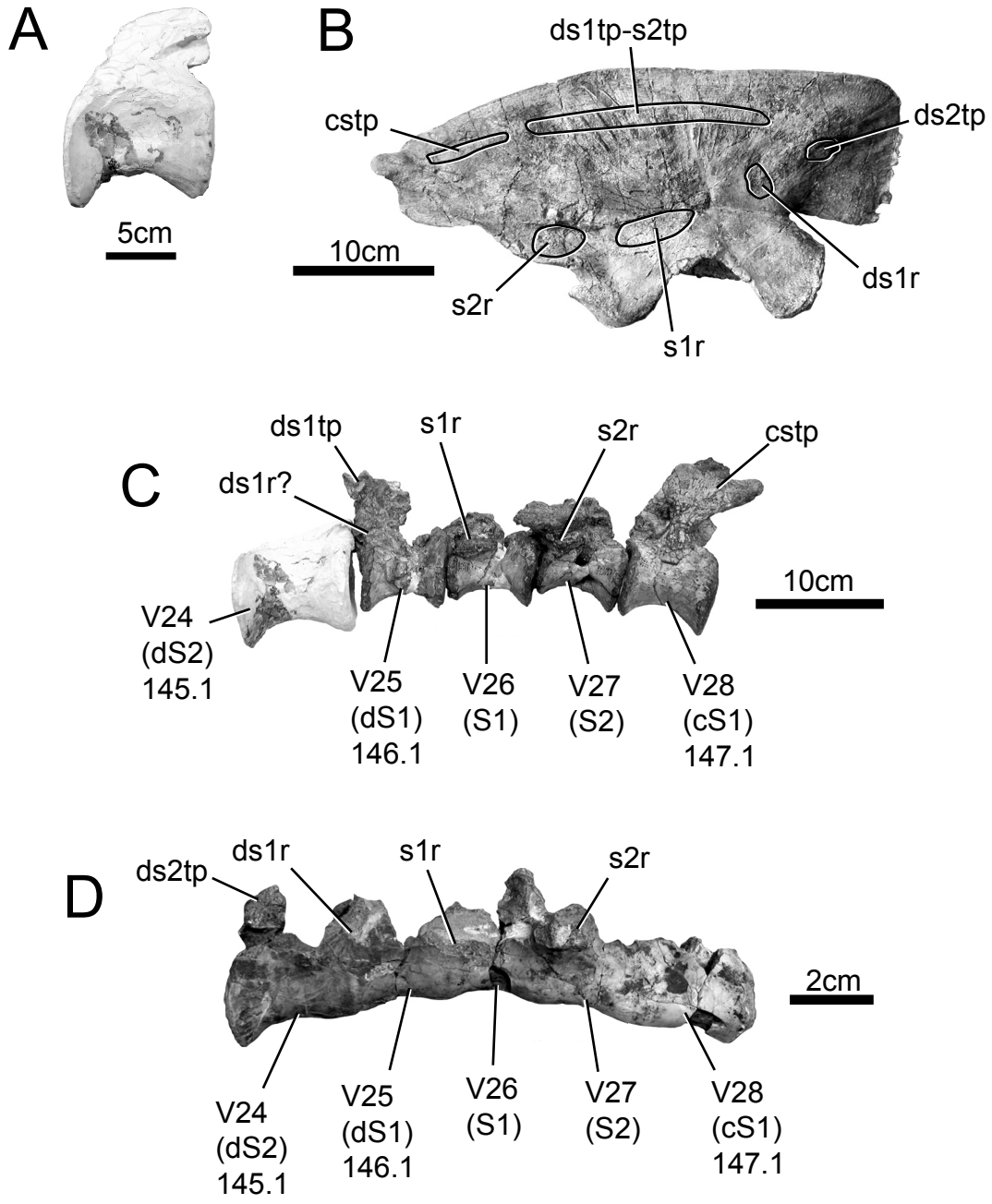


FIGURE 52. Coelophysoid sacra and ilial contacts. A, *Dilophosaurus* (UCMP 37302) 24th vertebra, probably dorsosacral 2, mostly reconstructed in plaster. B, *Dilophosaurus* (TMM 43646-60) left ilium, medial view. Rib and transverse process contacts indicated. C, *Dilophosaurus* (UCMP 37302) sacral vertebrae in left lateral and slightly ventral view. D, *"Syntarsus" kayentakatae* (TMM 43688-1) sacrum in left lateral view.

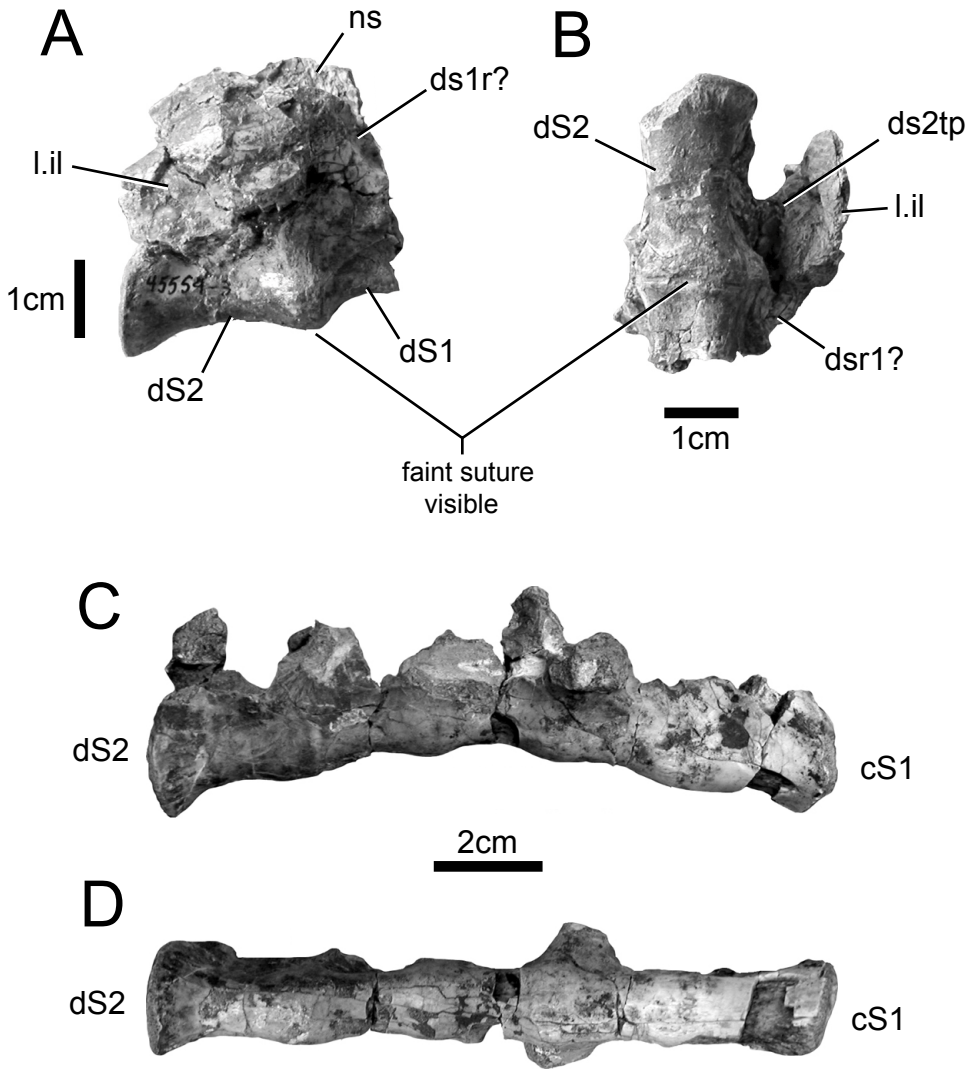


FIGURE 53. Sacral centra co-ossification. A, *Coelophysis* (TMM 45559-3) partial sacrum and ilium, left lateral view. B, same as A, ventral view. Specimen exhibits near-fusion of centra. C, *"Syntarsus" kayentakatae* (TMM 43688-1) in left lateral view. D, same as C, ventral view. Specimen exhibits complete fusion between centra, no visible sutural lines.

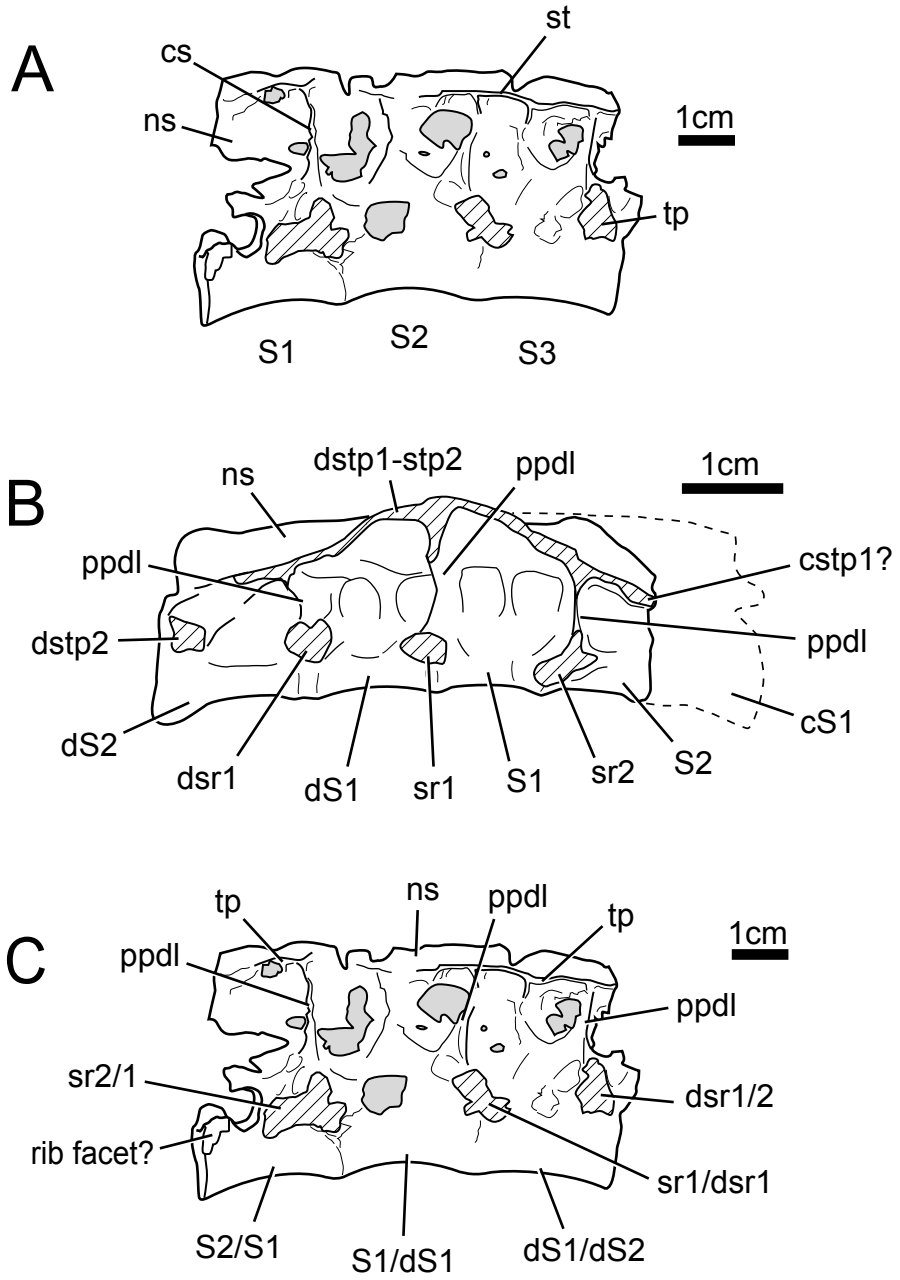


FIGURE 54. Sacrum of *Masiakasaurus*. A, *Masiakasaurus* (FMNH PR 2142) partial sacrum with components identified as per Carrano et al., (2002). B, Shake-N-Bake taxon (MCZ 9443) partial sacrum in left lateral view (after Tykoski and Rowe, 2004). C, *Masiaksaurus* (FMNH PR 2142) same as in A, with my interpretation of' sacral structures.

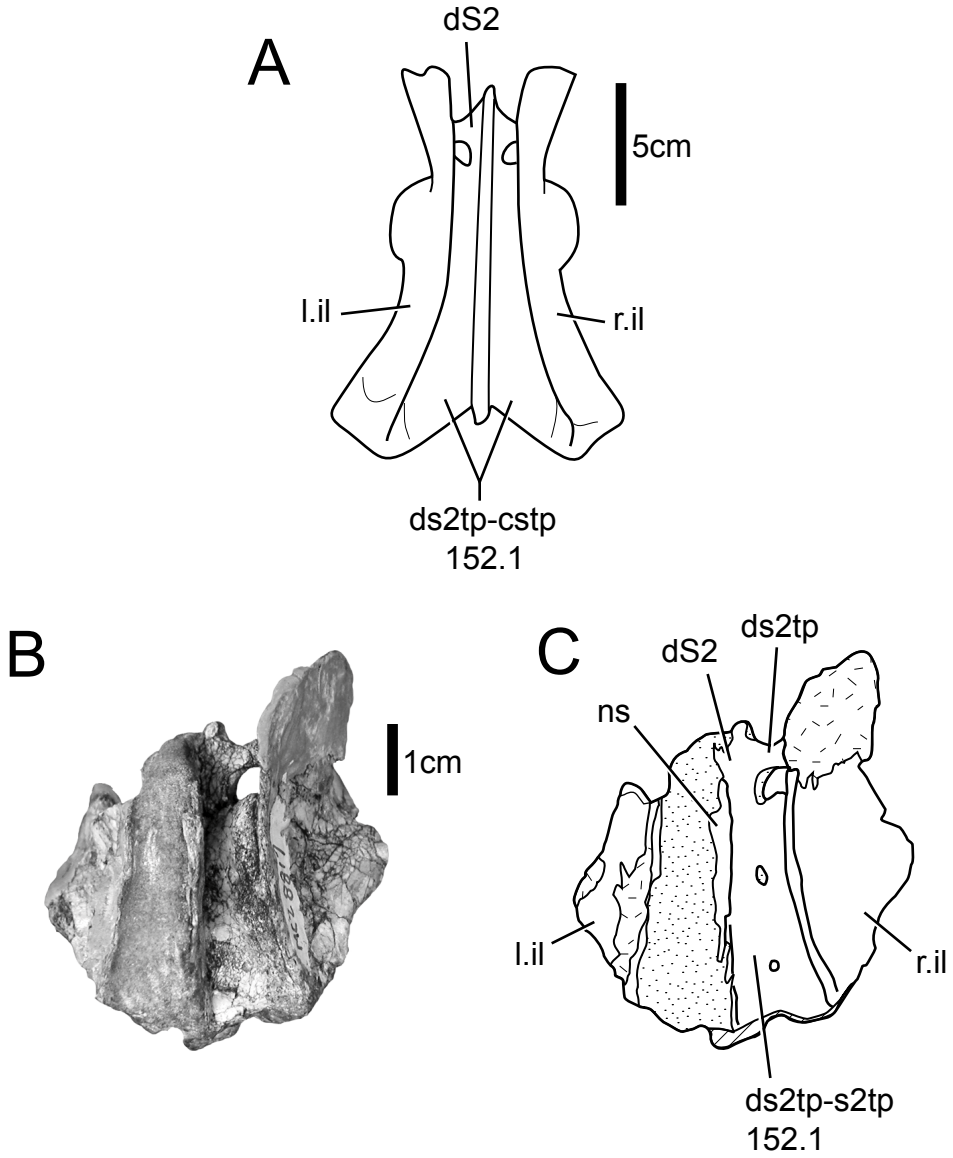


FIGURE 55. Sacral transverse process co-ossification. A, *Syntarsus rhodesiensis* synsacrum in dorsal view (after Raath, 1977). B, Shake-N-Bake taxon (MCZ 9442) partial synsacrum in dorsal view. C, line drawing of B. Stippling indicates sediment, cross-hatching indicates broken bone surface, and ticking indicates areas reconstructed or putty-filled.

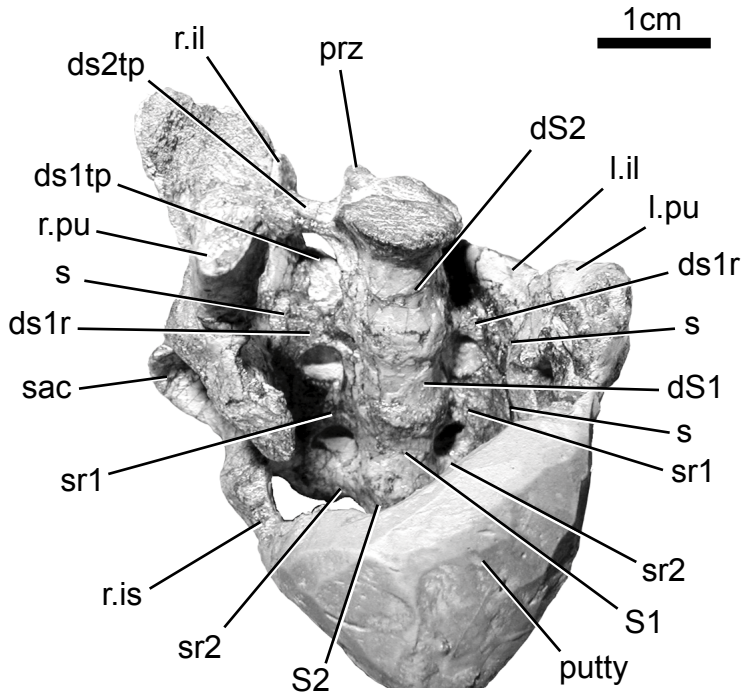


FIGURE 56. Coelophysoid synsacrum. Shake-N-Bake taxon (MCZ 9442), anteroventral view. Most of second sacral hidden from view by large mass of reconstructive putty used to stabilize parts of the puboischiadic plate.

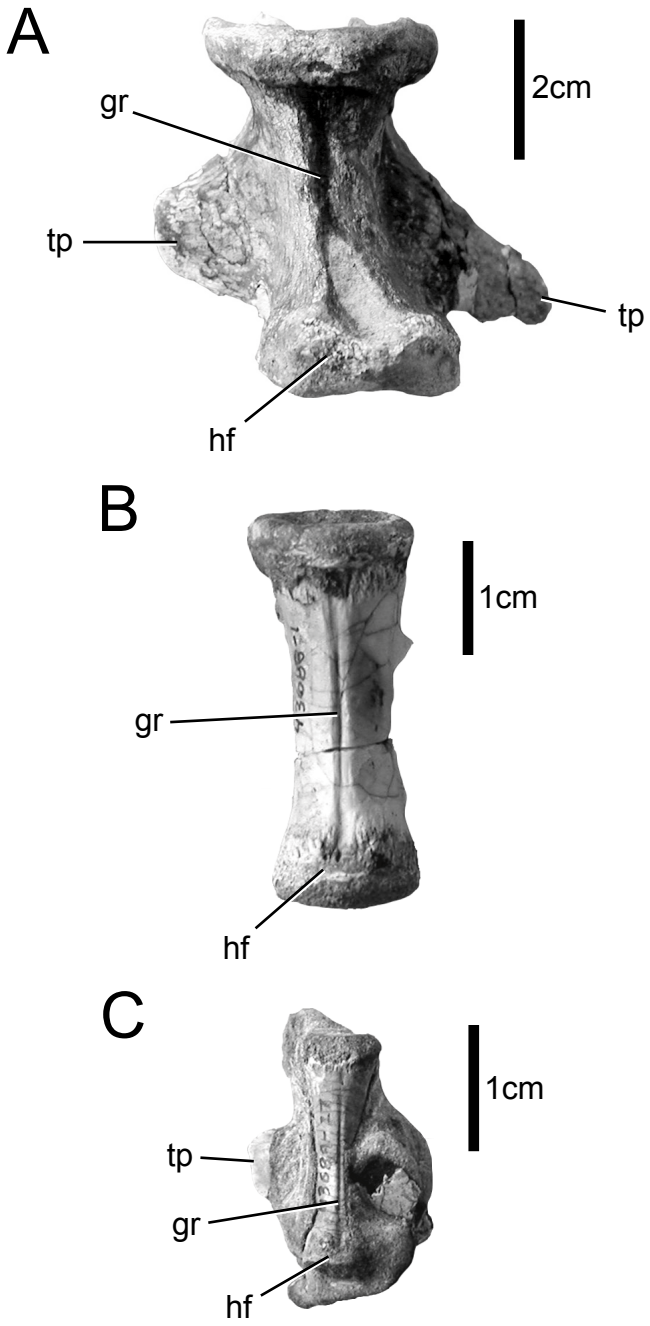


FIGURE 57. Coelophysoid caudal vertebrae with sharp ventral grooves. A, *Dilophosaurus* (TMM 43646-15). B, *"Syntarsus" kayentakatae* (TMM 43688-1). C, Shake-N-Bake taxon (TMM 43689-27). Shake-N-Bake caudal in C is still partially entombed in matrix. Anterior to top for all three specimens.

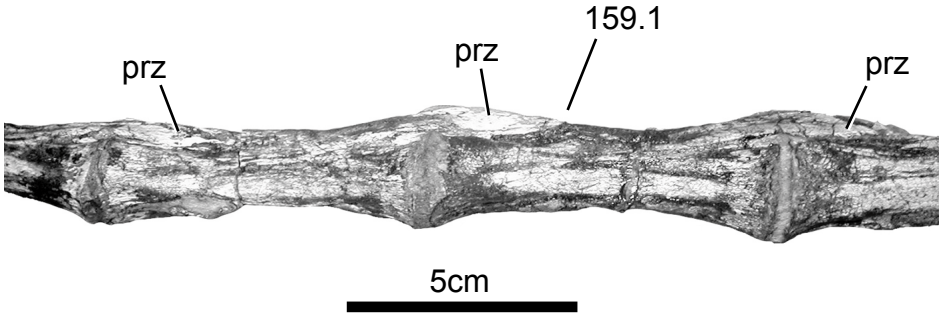


FIGURE 58. *Dilophosaurus* (TMM 43646-140) distal caudal vertebrae. Right lateral view. Prezygapaophyses overlap preceeding vertebral centrum by at least 25 percent centrum length.

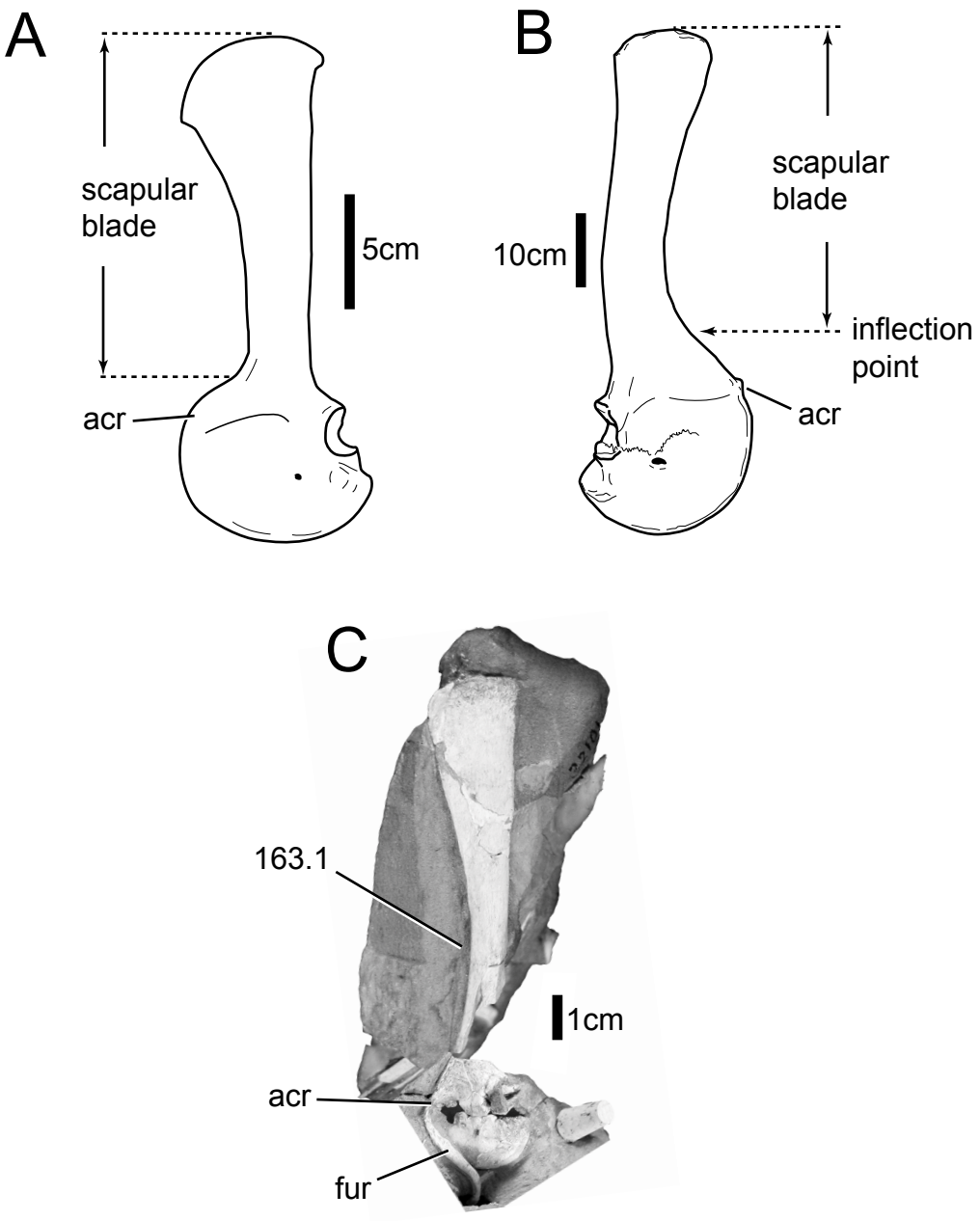


FIGURE 59. Theropod pectoral girdles and proportions of scapular blade. A, *"Syntarsus" kayentakatae* (MNA V2623) reconstructed left scapulocoracoid in lateral view. B, *Ceratosaurus* (UUVP 317) right scapulocoracoid in lateral view (after Madsen and Welles, 2000). C, *Segisaurus* (UCMP 32101) left pectoral girdle composite photograph in lateral view. Axes of upper and lower blocks may not be exactly aligned, but proportional relationships are maintained.

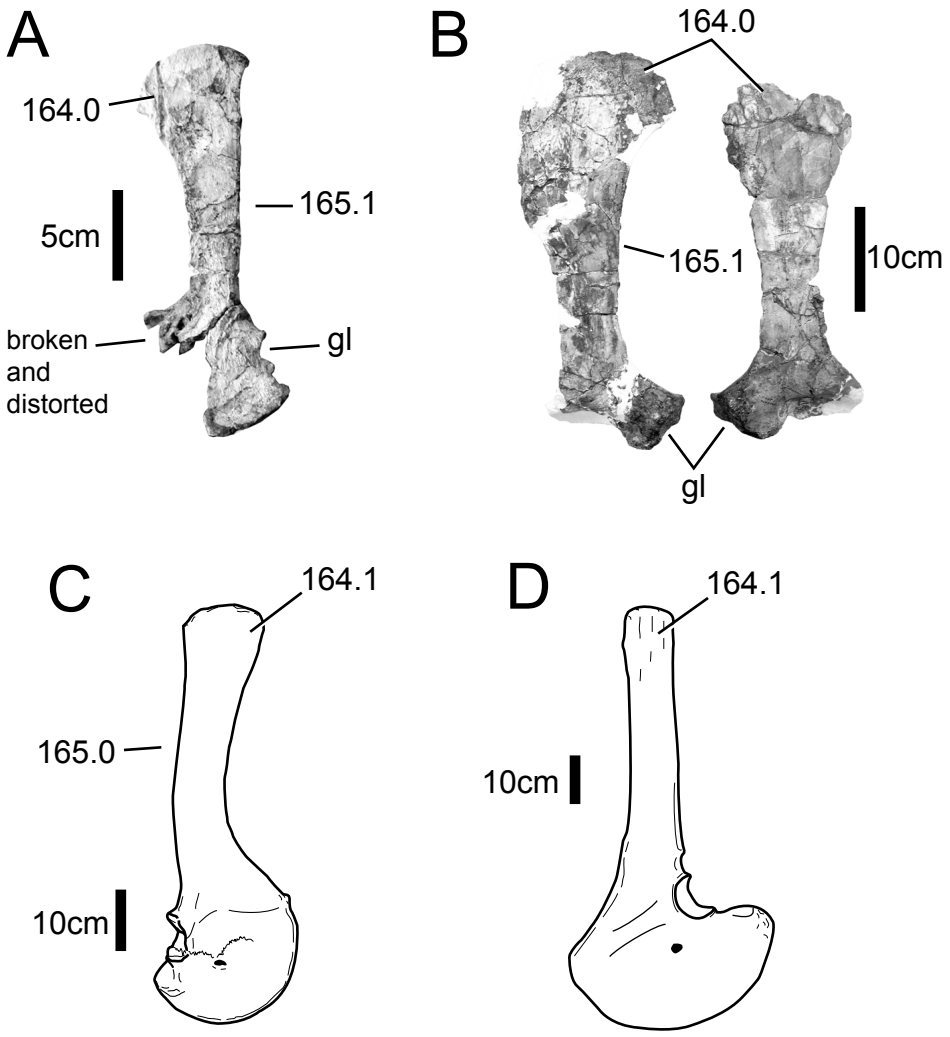


FIGURE 60. Distal expansion of theropod scapulae. A, *"Syntarsus" kayentakatae* (MNA V2623) partial right scapulocoracoid, reconstructed in medial view. B, *Dilophosaurus* (UCMP 37302) left and right scapulae, lateral view. C, *Ceratosaurus* (UUVP 317) right scapulocoracoid, lateral view (after Madsen and Welles, 2000). D, *Carnotaurus* (MACN-CH 894) left scapulocoracoid, lateral view (after Bonaparte et al., 1990).

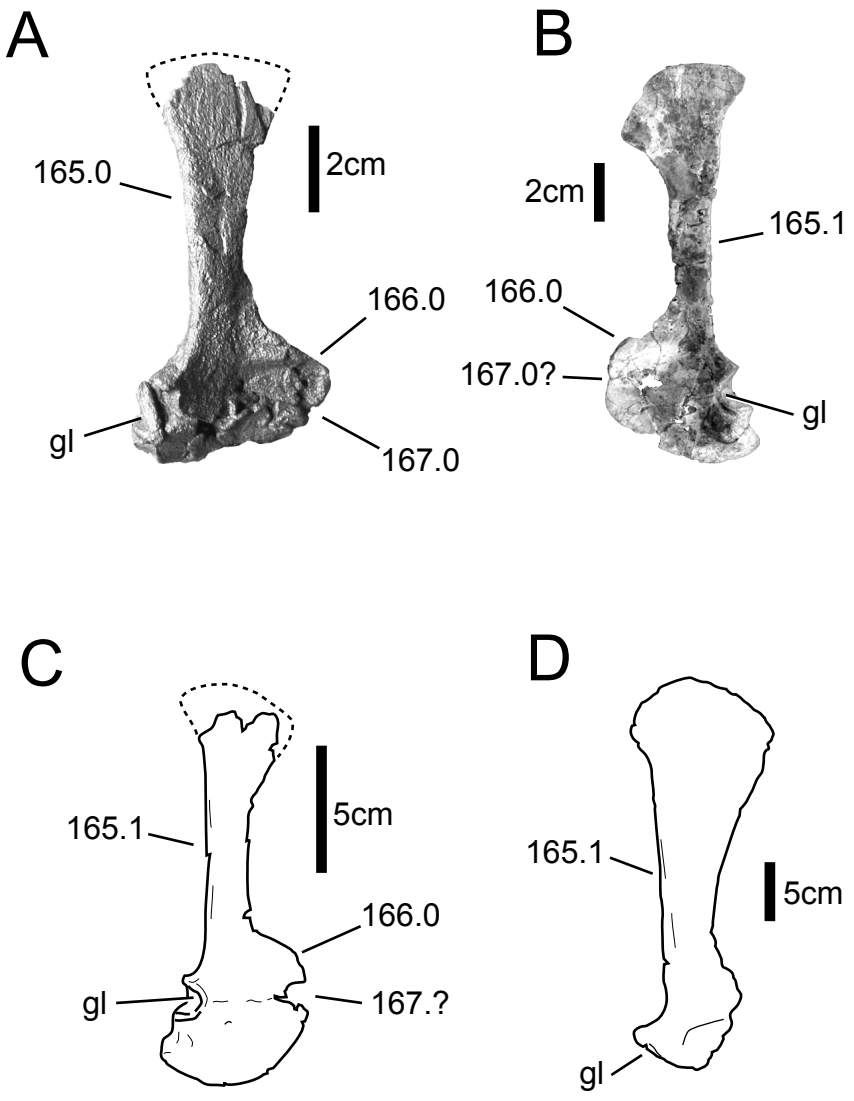


FIGURE 61. Scapulae of *Eoraptor* and coelophysoids. A, *Eoraptor* (cast of PVSJ 512) right scapula, lateral view. B, *Coelophysis* (CMNH 11895) left scapulocoracoid, lateral view. C, *Syntarsus rhodesiensis* (QG 143) right scapulocoracoid, lateral view. D, *Gojirasaurus* (UCM 47221) partial right scapula, lateral view.

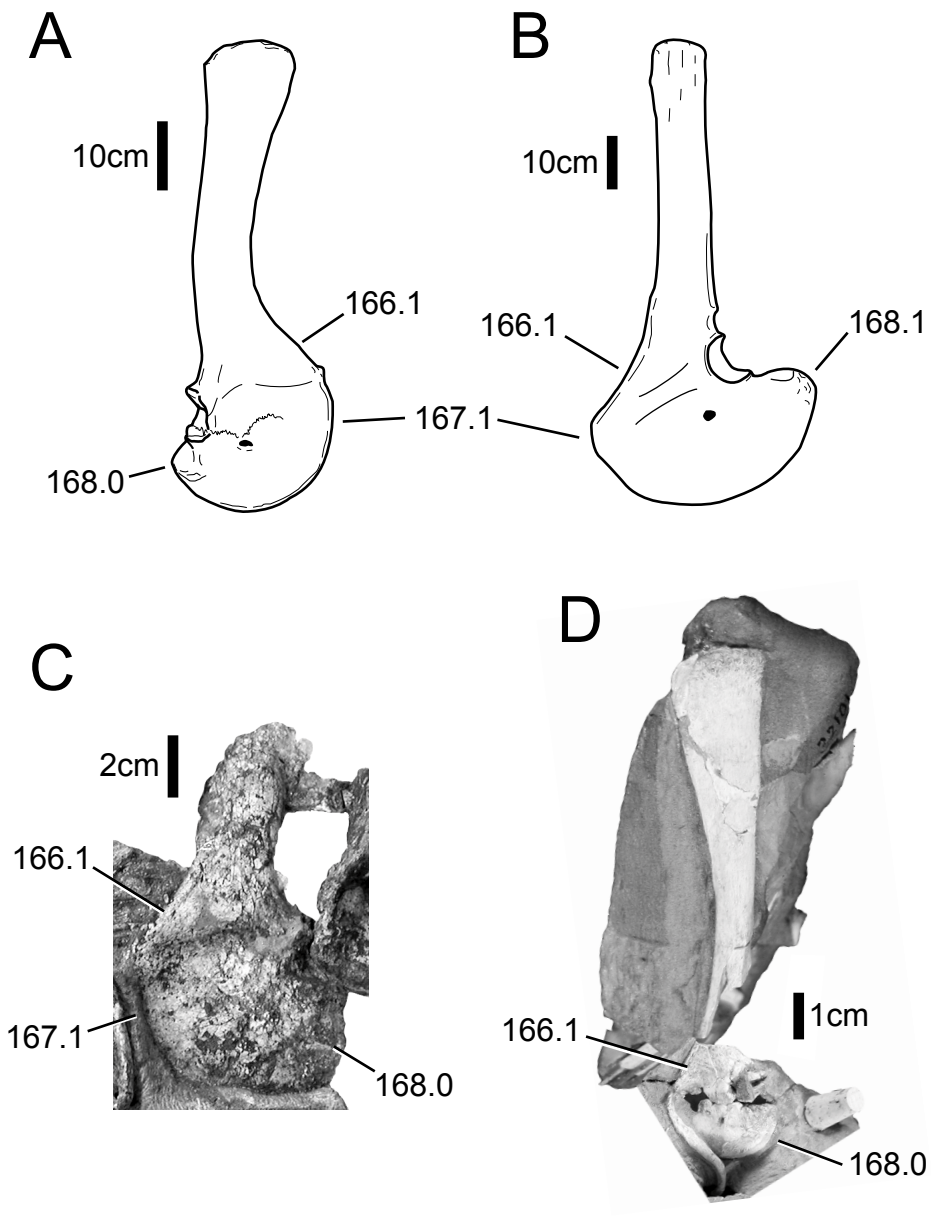


FIGURE 62. Theropod scapulae. A, *Ceratosaurus* (UUVP 317) right scapulocoracoid, lateral view (after Madsen and Welles, 2000). B, *Carnotaurus* (MACN-CH 894) left scapulocoracoid, lateral view (after Bonaparte et al., 1990). C, *"Syntarsus" kayentakatae* (MNA V2623) partial left scapulocoracoid, lateral view. D, *Segisaurus* (UCMP 32101) left pectoral girdle, lateral view.

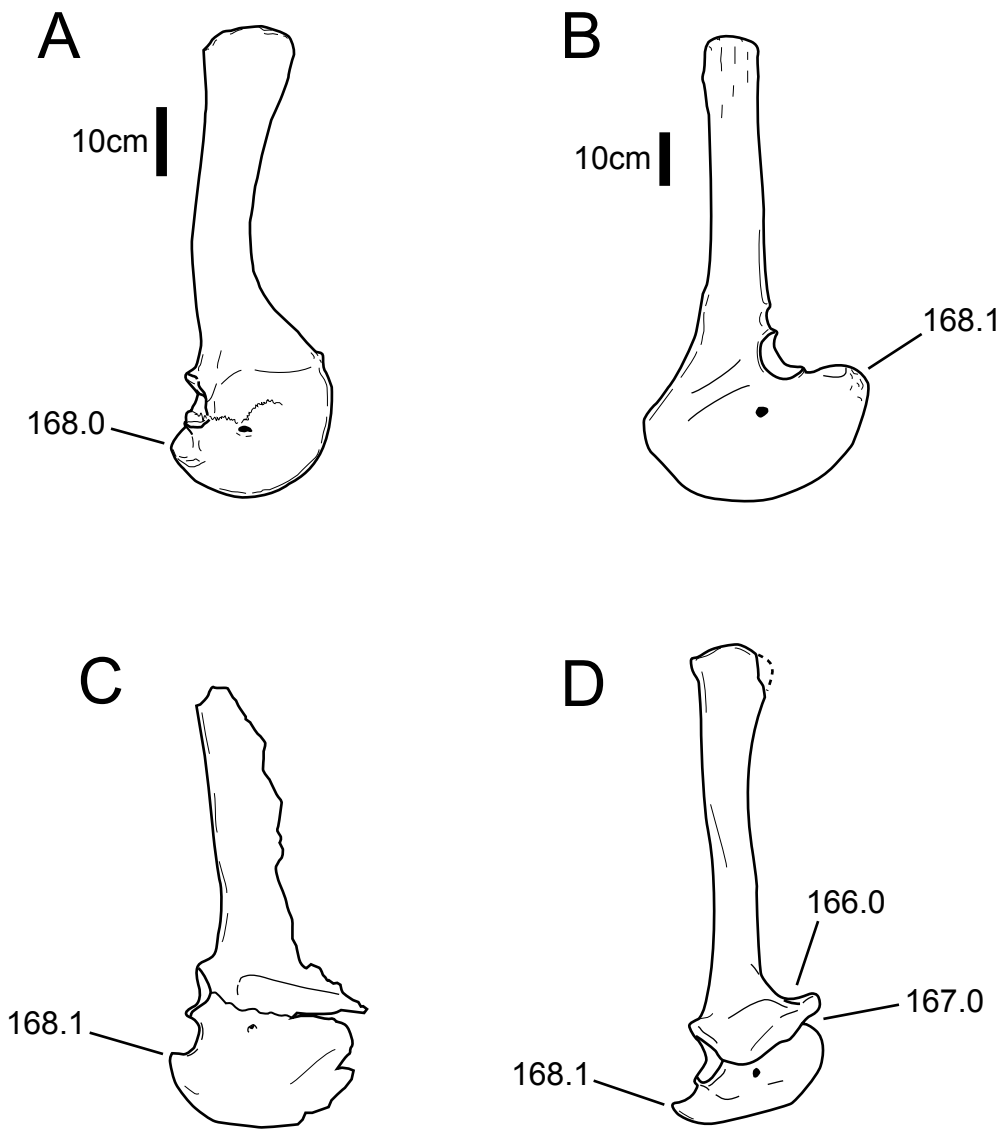


FIGURE 63. Theropod scapulae. A, *Ceratosaurus* (UUVP 317) right scapulocoracoid, lateral view (after Madsen and Welles, 2000). B, *Carnotaurus* (MACN-CH 894) left scapulocoracoid, lateral view (after Bonaparte et al., 1990). C, *Elaphrosaurus* (MB not numbered) right scapula and coracoid, lateral view (after Janensch, 1925). D, *Allosaurus* (USNM 4734) right scapula and coracoid, lateral view (after Gilmore, 1920).

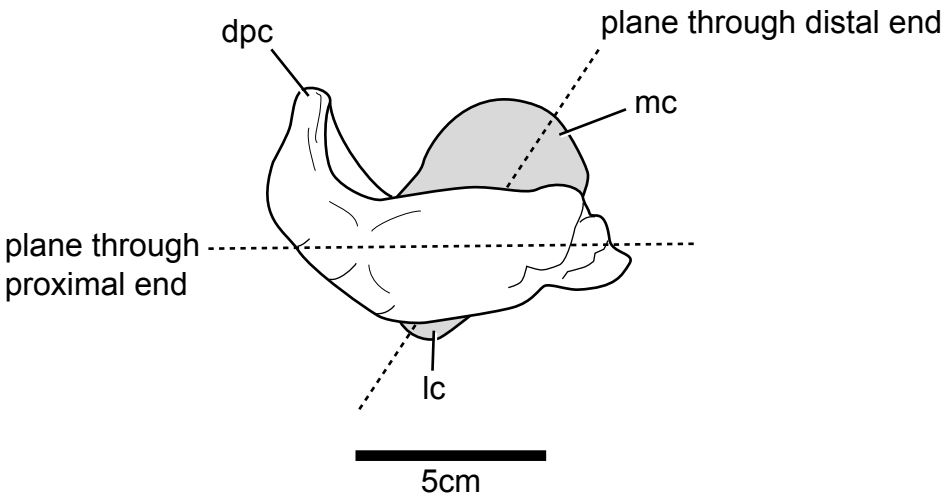


FIGURE 64. Humeral torsion. Left humerus of Dilophosaurus (UCMP 37302) in proximal view (after Welles, 1984). Shaded areas indicate outline of distal end of humerus. Dotted lines approximate planes of greatest width through the proximal and distal parts of the humerus. This specimen provides an example of state 1 for character 200 of the phylogenetic analysis.

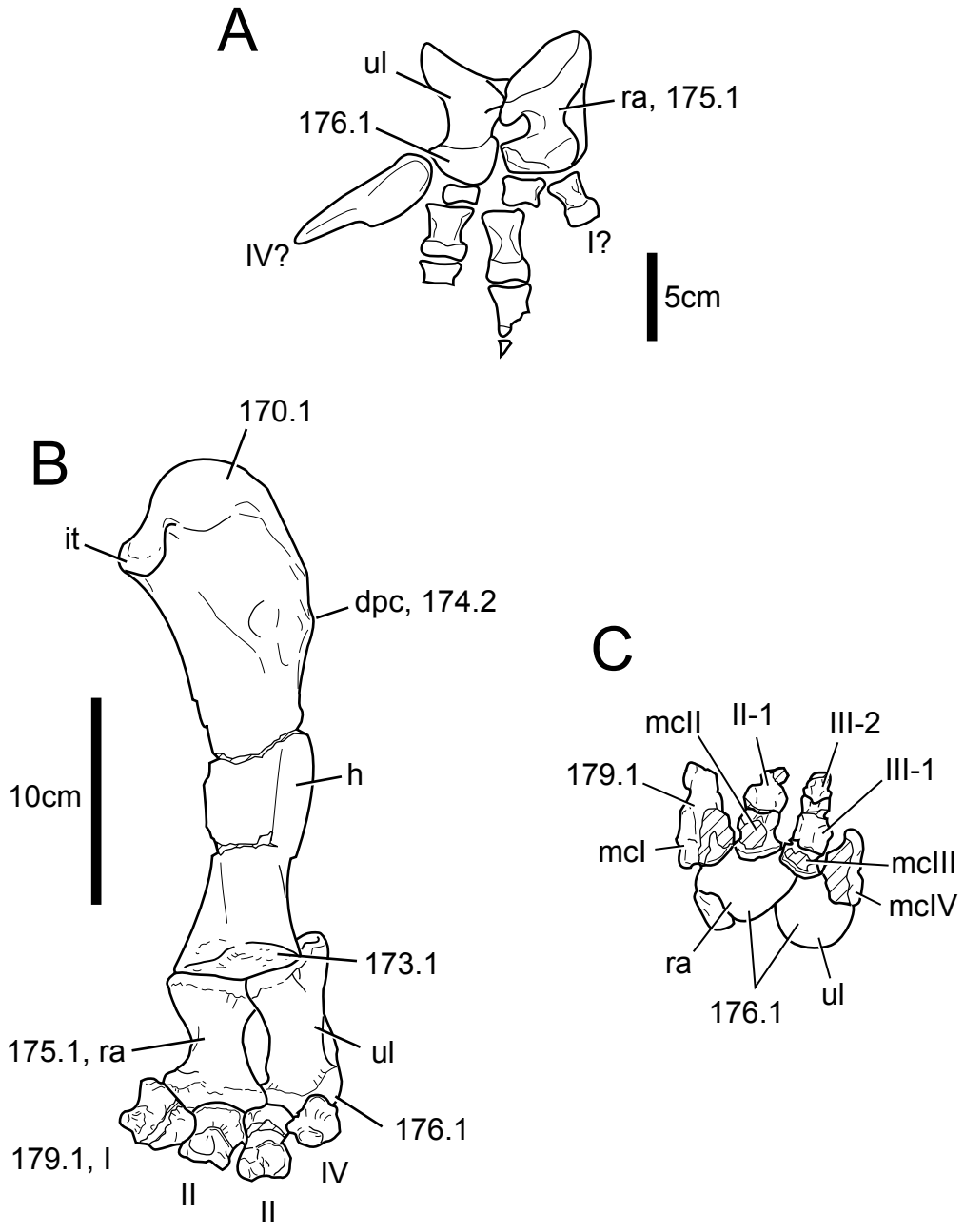


FIGURE 65. Abelisaur forelimbs. A, *Carnotaurus* (MACN-CH 894) radius, ulna, and manus in ventral (palmer) view (after Bonaparte et al., 1990). These were described as the right side elements, but that identification may be incorrect. B, *Aucasaurus* (MCF-PVPH-236) right forelimb, posterior/ventral view. C, same as in B, distal view, showing hemispherical articular surfaces of radius and ulna (after Coria et al., 2002) Scale same as in B.

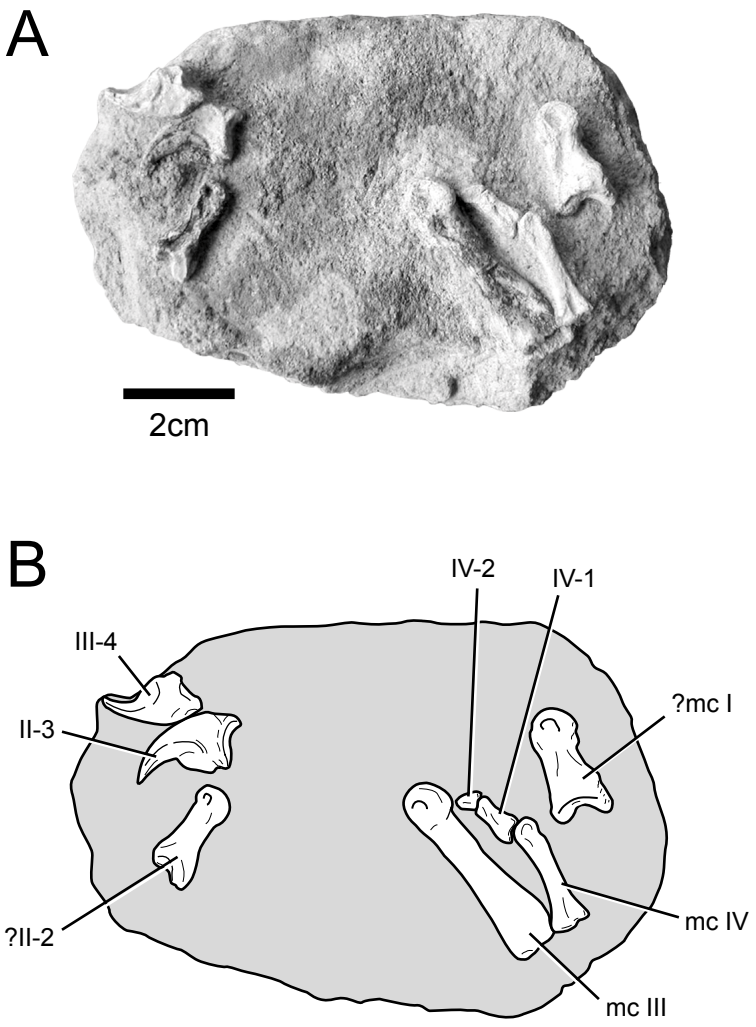


FIGURE 66. Manus elements of *"Syntarsus" kayentakatae*. A, associated manus pieces of MNA V2623. B, line drawing of A. Abbreviations with question marks indicate tentative identifications.

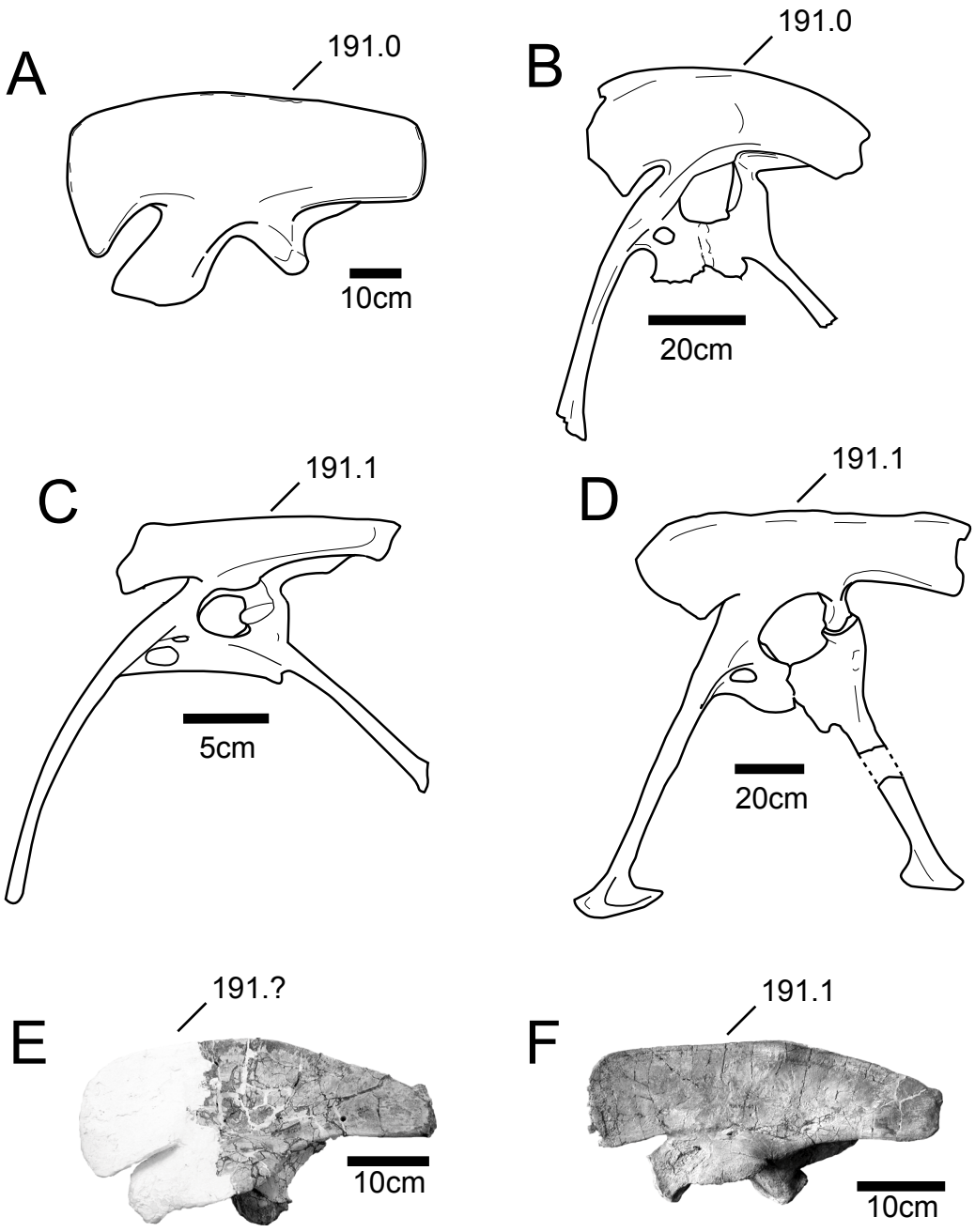


FIGURE 67. Dorsal margin of theropod ilia. All left side elements, lateral view. B-D include co-ossified pubis and ischium. A, *Allosaurus* (after Madsen, 1976). B, *Ceratosaurus* (USNM 4735) (after Gilmore, 1920). C, *Syntarsus rhodesiensis* (after Raath, 1977). D, *Carnotaurus* (MACN-CH 894) (after Bonaparte et al., 1990). E, *Dilophosaurus* (UCMP 37302). F, *Dilophosaurus* (TMM 43646-60).

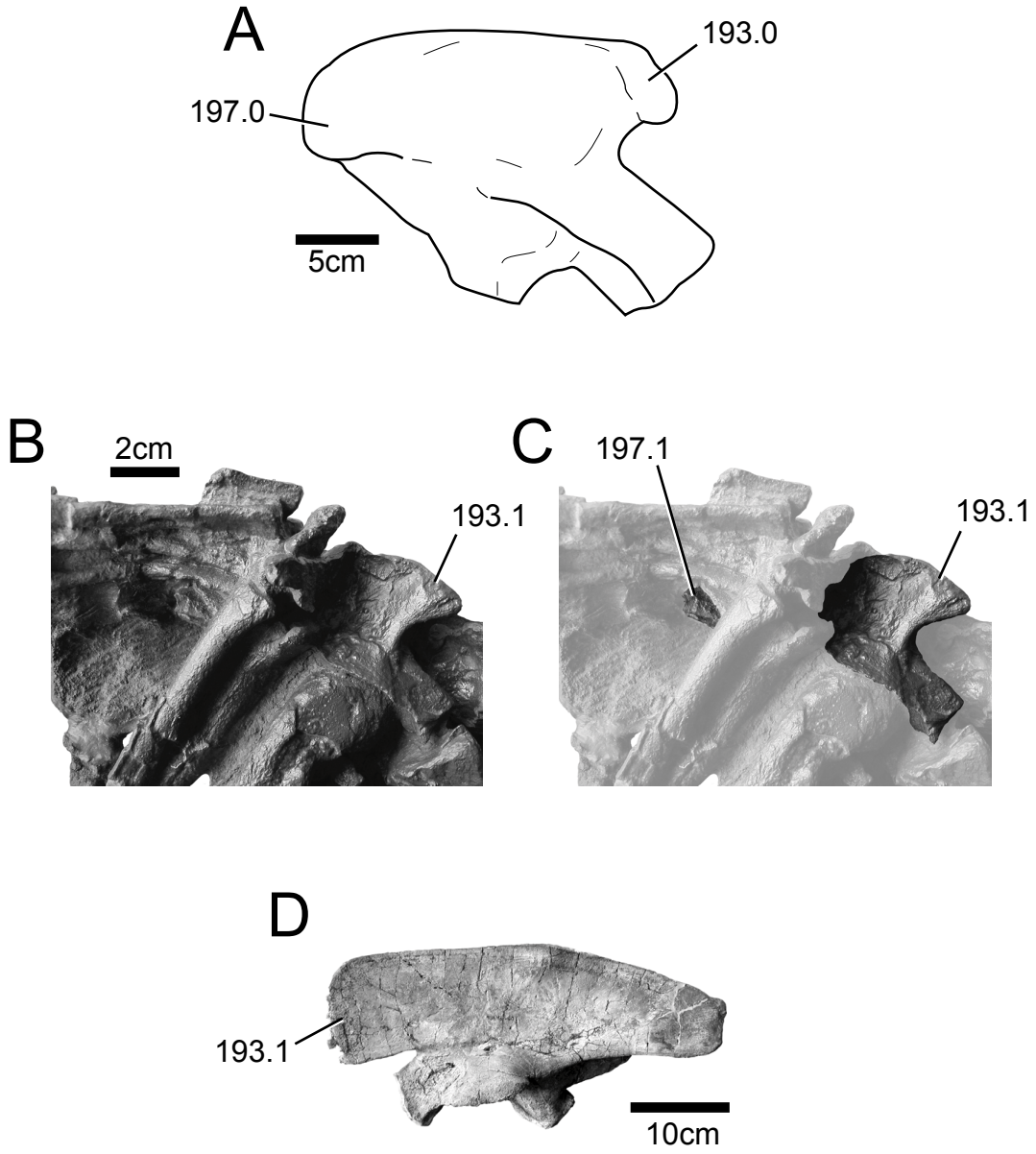


FIGURE 68. Preacetabular process of ilium. A, *Herrerasaurus* reconstruction of right ilium (based upon PVL 2566), lateral view (after Novas, 1993). B, *Eoraptor* (TMM 43451-2; cast of PVSJ 512) right pelvis and hindlimb elements. C, same as in B, with ilium highlighted for clarity. D, *Dilophosaurus* (TMM 43646-60) left ilium, lateral view.

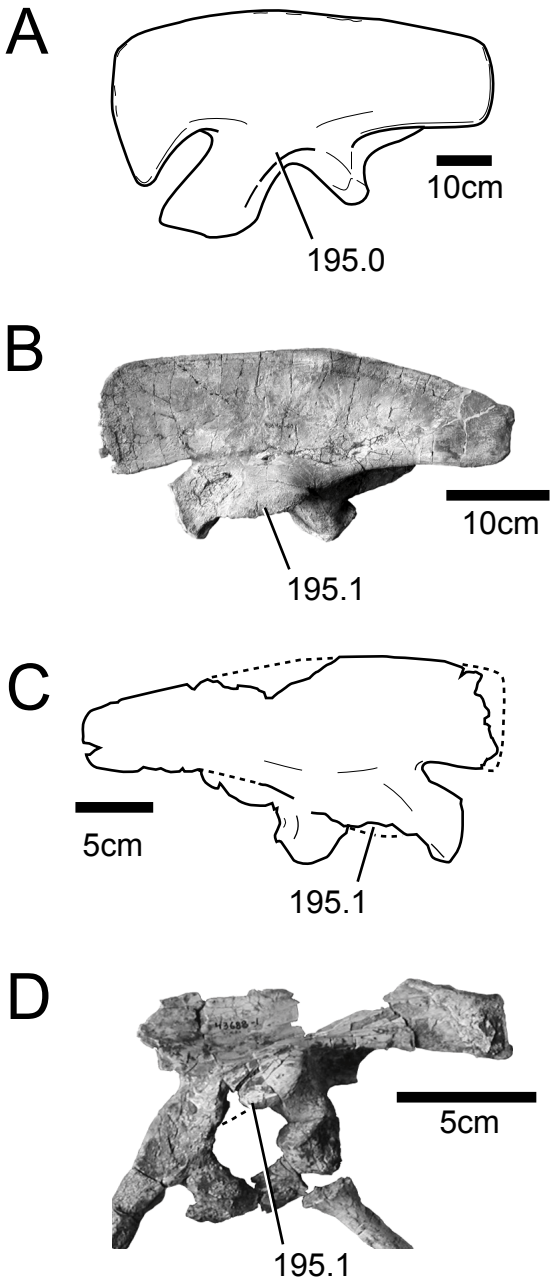


FIGURE 69. Supraacetabular crest. A, *Allosaurus* left ilium, lateral view (after Madsen, 1976). B, *Dilophosaurus* (TMM 43646-60) left ilium, lateral view. C, *Liliensternus* (MB 2175.4.1) right ilium, lateral view (after Huene, 1934). D, *"Syntarsus" kayentakatae* (TMM 43688-1) partial left pelvic girdle, close-up of acetabular region.

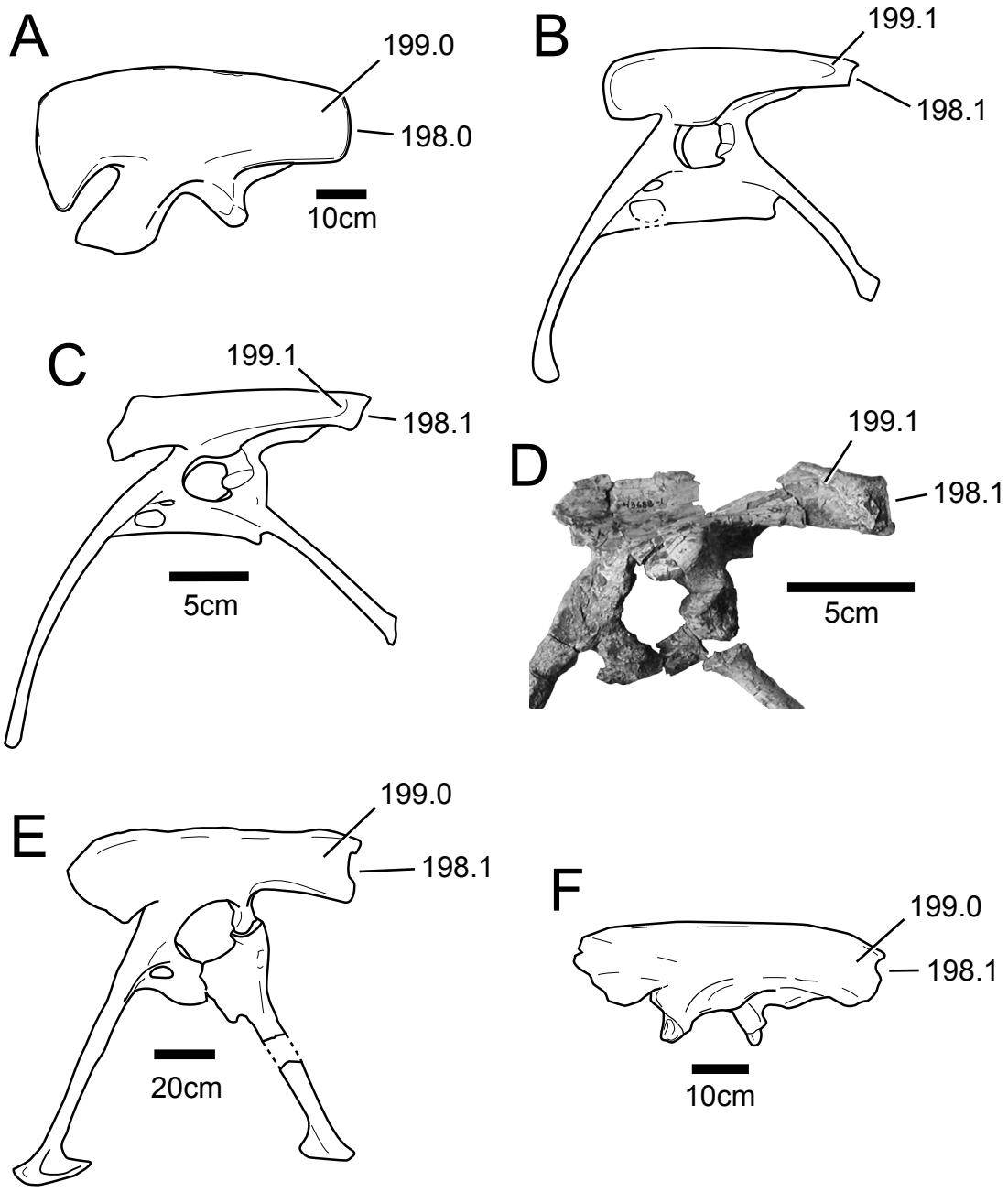


FIGURE 70. Theropod ilia and pelves. All left side elements, lateral view. A, *Allosaurus* ilium (after Madsen, 1976). B, *Coelophysis* (after Rowe and Gauthier, 1990). C, *Syntarsus rhodesiensis* (after Raath, 1977, 1990). D, *"Syntarsus" kayentakatae* (TMM 43688-1) partial pelvis. E, *Carnotaurus* (MACN-CH 894) (after Bonaparte et al., 1990). F, *Majungatholus* (UA 8678) ilium (after Sampson et al., 1998).

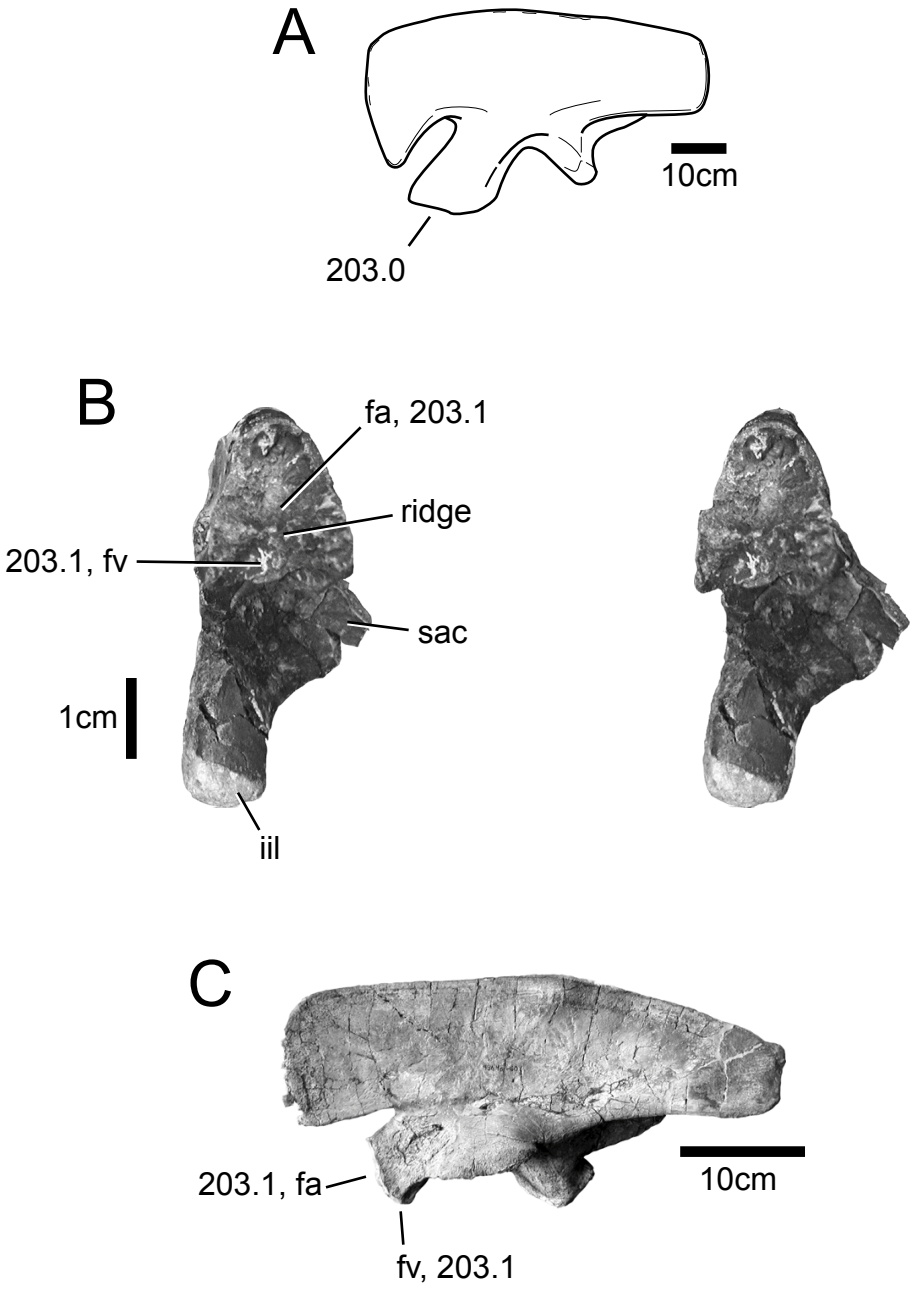


FIGURE 71. Ilio-pubic contact morphology and orientation. A, *Allosaurus* left ilium, lateral view (after Madsen, 1976). B, *"Syntarsus" kayentakatae?* (UCMP 128659) stereophotograph of partial left ilium of juvenile individual, ventral view. C, *Dilophosaurus* (TMM 43646-60) left ilium, lateral view. Two facet-contact between ilium and pubis visible in B and C.

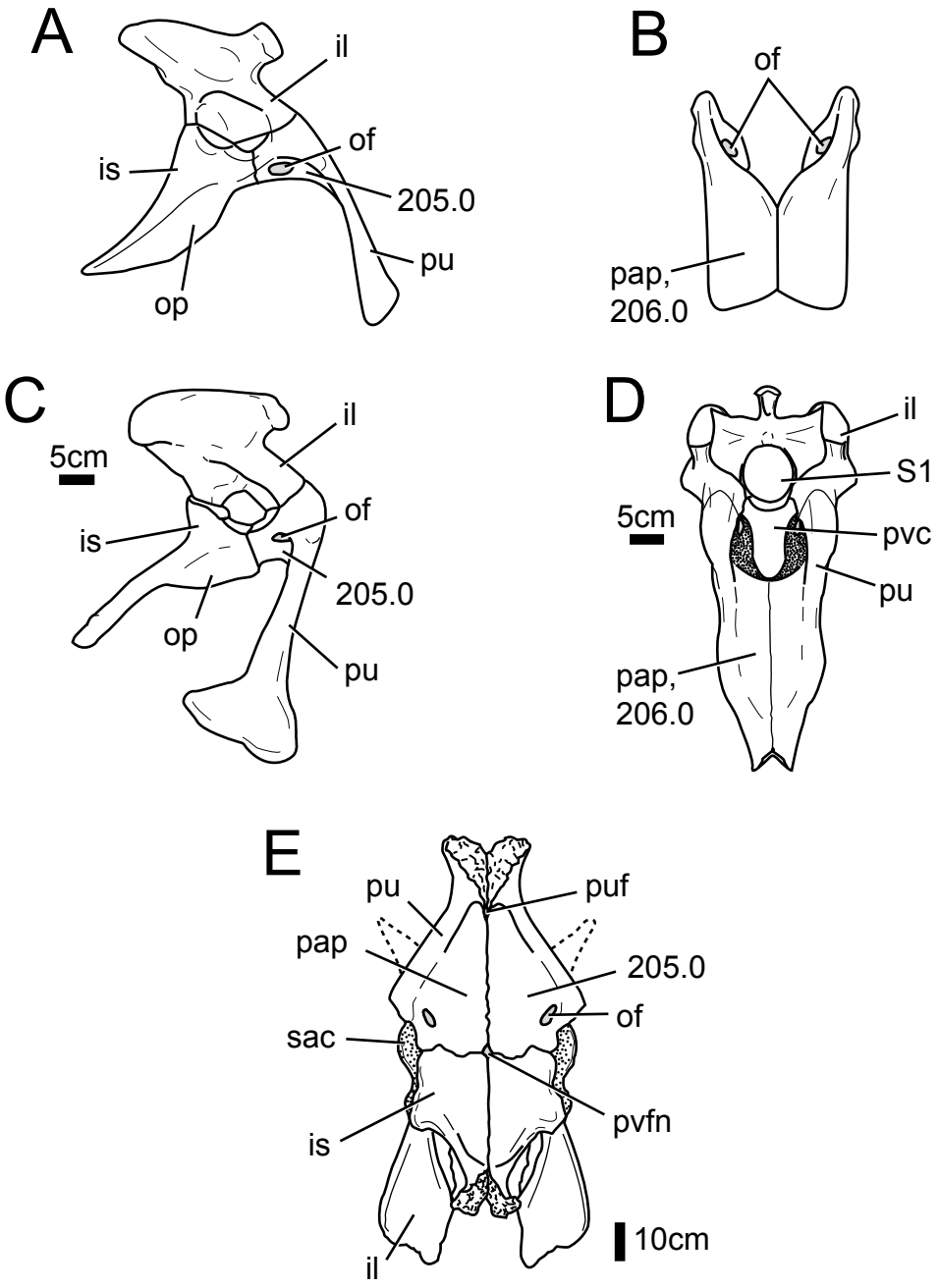


FIGURE 72. Evolution of the pubo-ischiadic plate. A, *Marasuchus* right side pelvis, lateral view (after Sereno and Arcucci, 1994). B, *Marasuchus* pubes, anterior view (after Sereno and Arcucci, 1994). C, *Herrerasaurus* right side pelvis, lateral view (after Novas, 1993). D, same as in C, anterior view. E, *Torvosaurus* pelves (BYU 2013-2015), ventral view, anterior to top (after Galton and Jensen, 1979). Openings through the pubo-ischiadic plate indicated by light gray fill.

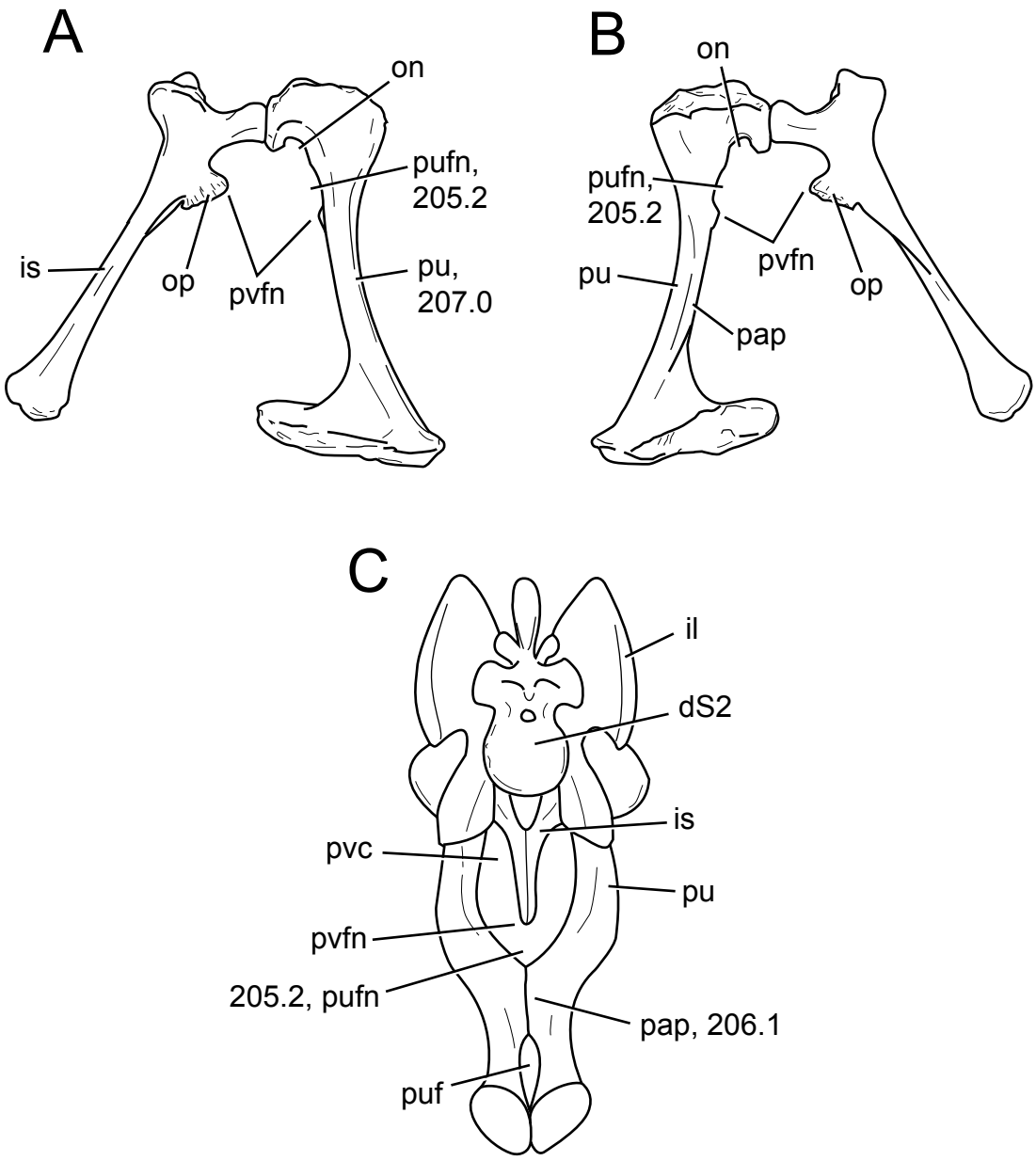


FIGURE 73. Evolution of the pubo-ischiadic plate. A, *Allosaurus* right ischium and pubis, lateral view (after Madsen, 1976). B, same as in A, medial view. C, *Allosaurus* sacrum and pelves, anterior view (after Molnar et al., 1990).

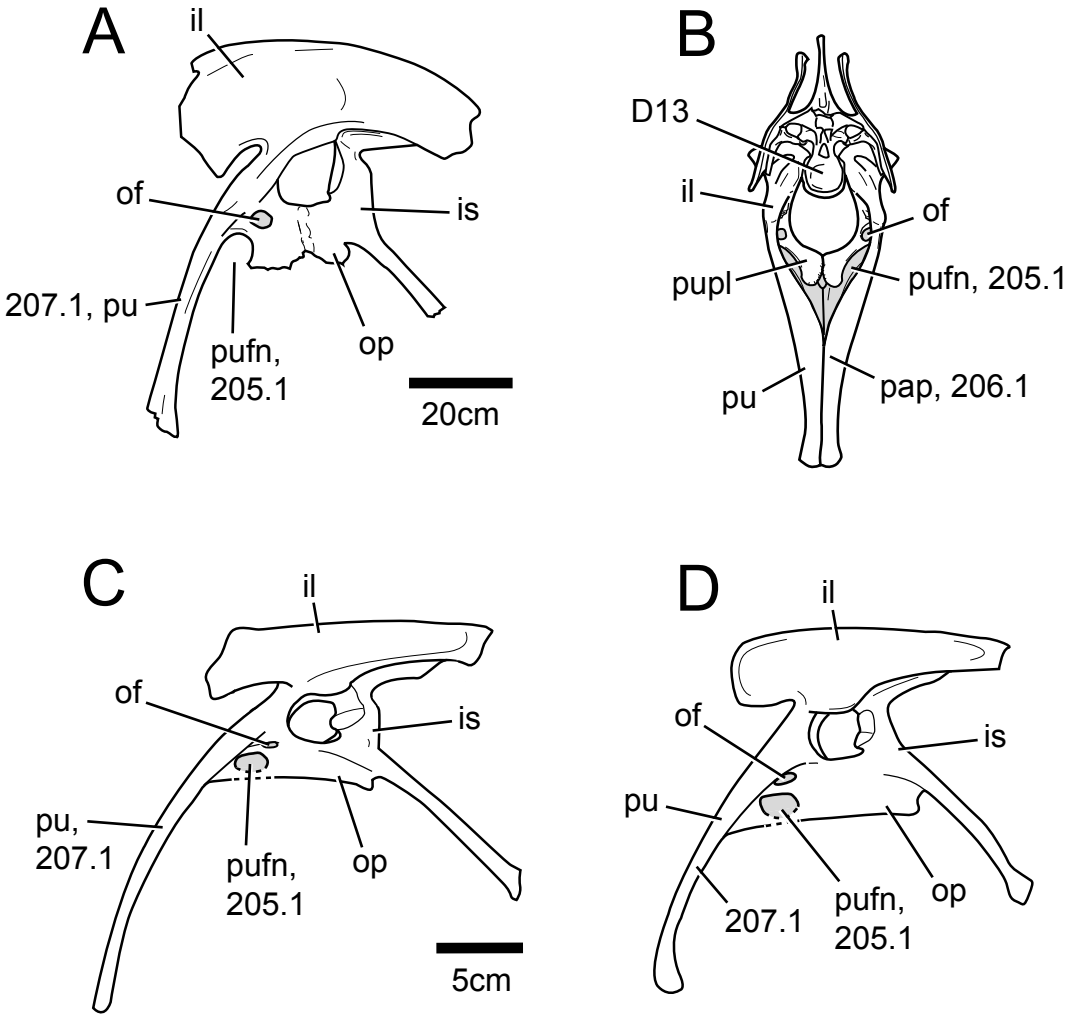


FIGURE 74. Evolution of the pubo-ischiadic plate. A, *Ceratosaurus* (USNM 4735) left pelvis, lateral view (after Gilmore, 1920). B, *Ceratosaurus* (USNM 4735) pelves and sacrum, anterior view. Note that distal end of pubes were illustrated as restored in exhibit mount, but were not recovered with specimen (after Gilmore, 1920). C, *Syntarsus rhodesiensis* (QG 1) left pelvis, lateral view (after Raath, 1969, 1977, 1990). D, *Coelophysis* left pelvis, lateral view (after Rowe and Gauthier, 1990).

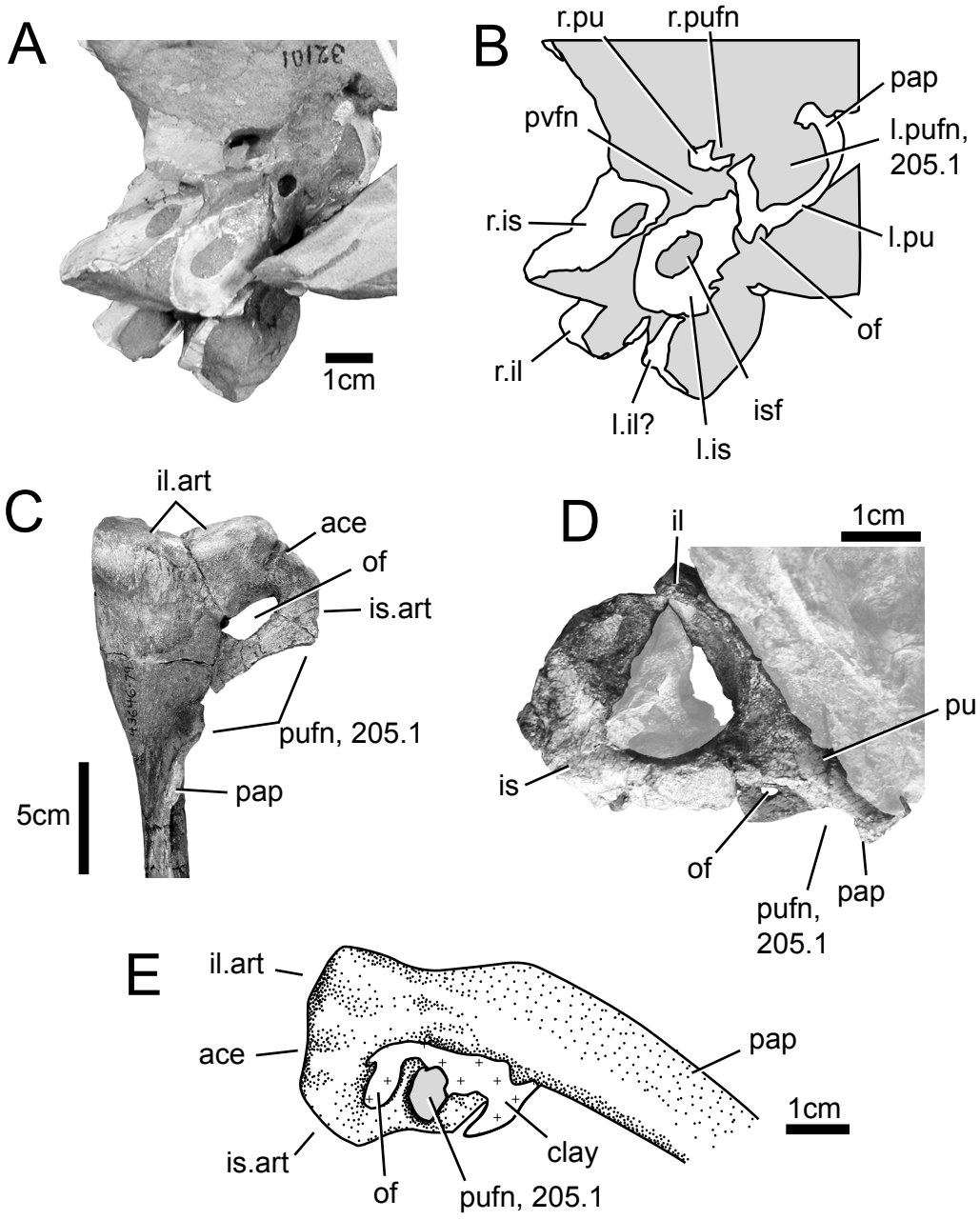


FIGURE 75. Evolution of the pubo-ischiadic plate. A, *Segisaurus* (UCMP 32101) pelves in ventral and slightly posterolateral view. Anterior to top right. B, line drawing of A. Shaded areas indicate sediment. C, *Dilophosaurus* (TMM 43646-79) proximal right pubis, medial view. D, Shake-N-Bake taxon (MCZ 9443) right pelvis, lateral view (non-pelvic elements shaded). E, *Eoraptor* (drawn from cast of PVSJ 512) right pubis, ventrolateral and slightly anterior view.

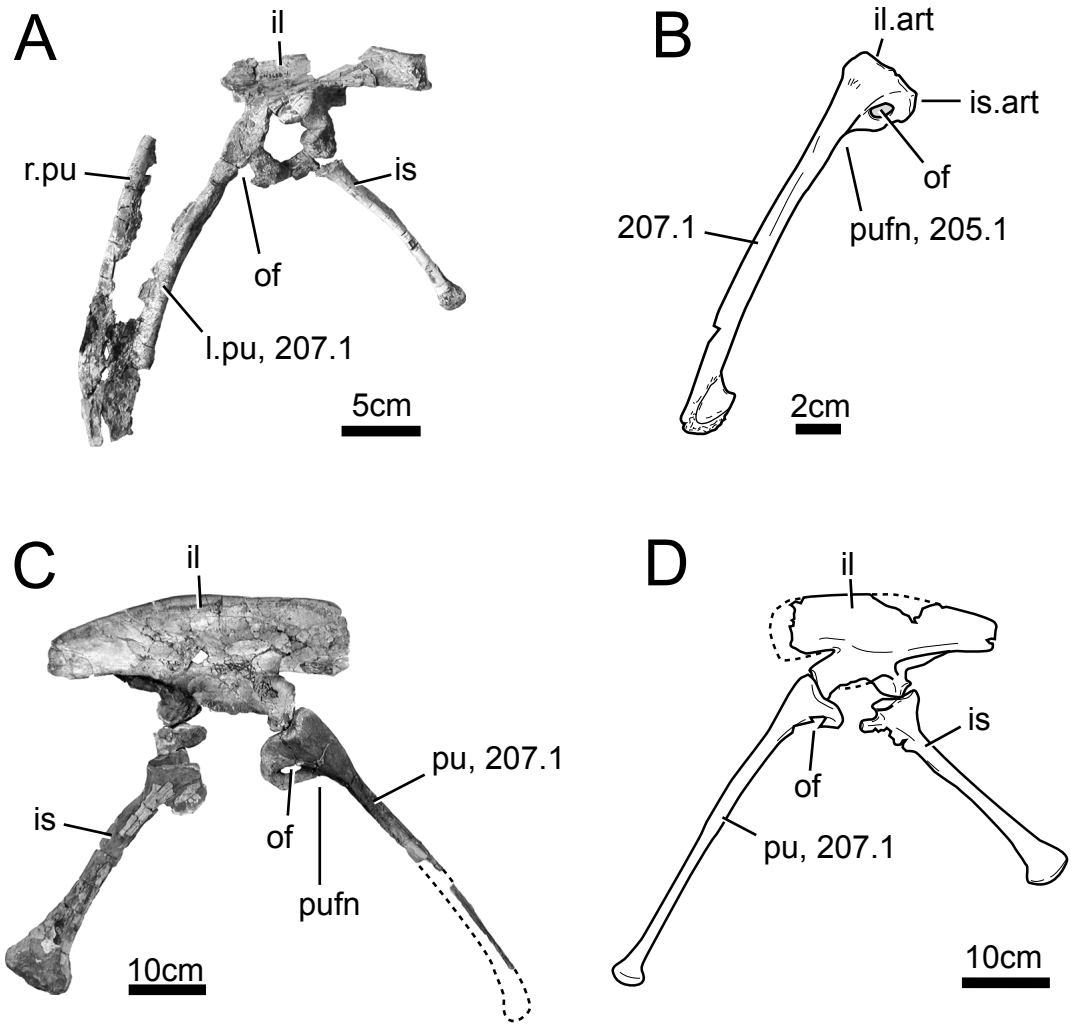


FIGURE 76. Pubis with anteriorly convex shaft. A, *"Syntarsus" kayentakatae* (TMM 43688-1) left pelvis and partial right pubic shaft, left lateral view. B, *Masiakasaurus* (FMNH PR 2108) left pubis, lateral view (after Carrano et al., 2002). C, *Dilophosaurus* (TMM 43646-26, 43646-33, 43646-59, 43646-79) right pelvis, lateral view. Dotted lines indicate reconstruction of distal pubic shaft based upon recently found but not yet prepared pieces of TMM 43646-79. D, *Liliensternus* (MB.R.2175) left pelvis, lateral view (after Huene, 1934).

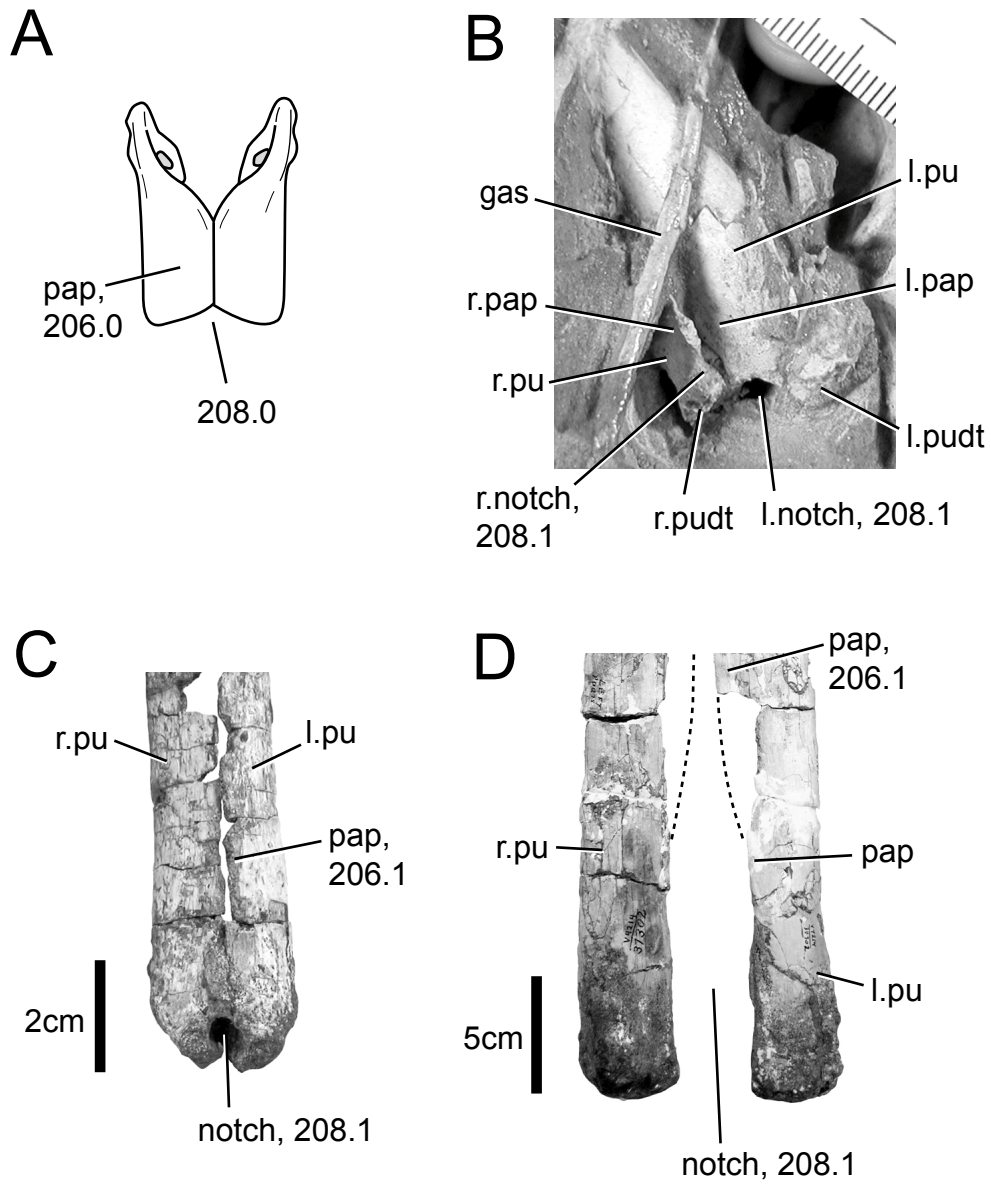


FIGURE 77. Distal pubes separation. A, *Marasuchus* pubes in anterior view (after Sereno and Arcucci, 1994). B, *Segisaurus* (UCMP 32101) distal pubes, anterior and left lateral view. Scale bar in photo in millimeters. C, *"Syntarsus" kayentakatae* (MNA V2623) distal pubes, anterior view. D, *Dilophosaurus* (UCMP 37302) distal pubes, anterior view. Left pubis mislabeled as right and visa versa in UCMP collections. Dotted lines show reconstructed medial margins of right and left pubes, and would together form pubic apron.

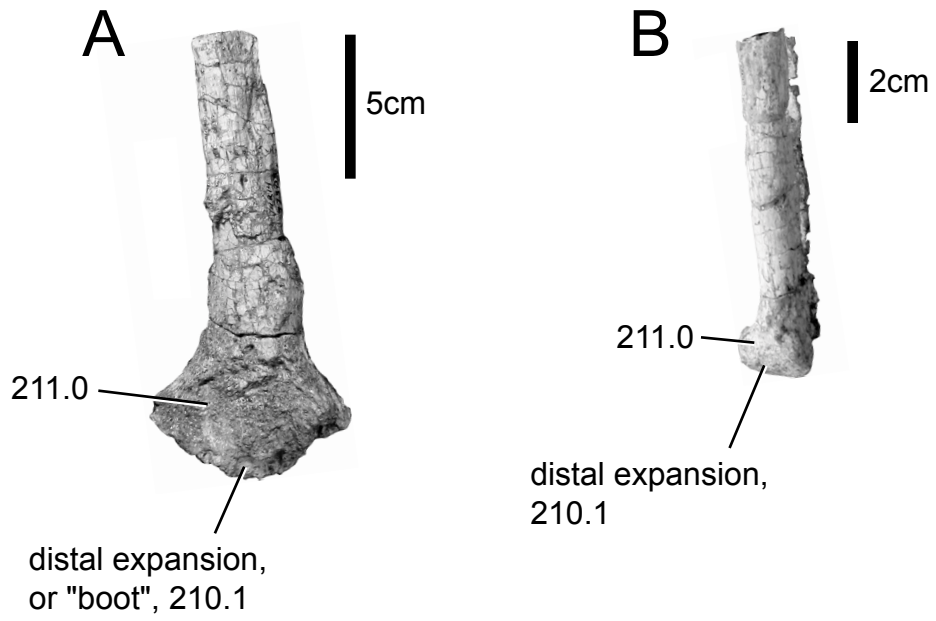


FIGURE 78. Coelophysoid distal pubic expansion. A, *Dilophosaurus* (UCMP 37303) right distal pubis, lateral view. B, *"Syntarsus" kayentakatae* (MNA V2623) right and left distal pubes, right lateral view. Anteroposterior thickness of pubic shafts in B appears larger than actually is because of anterior-ward distortion of medial margins of pubes.

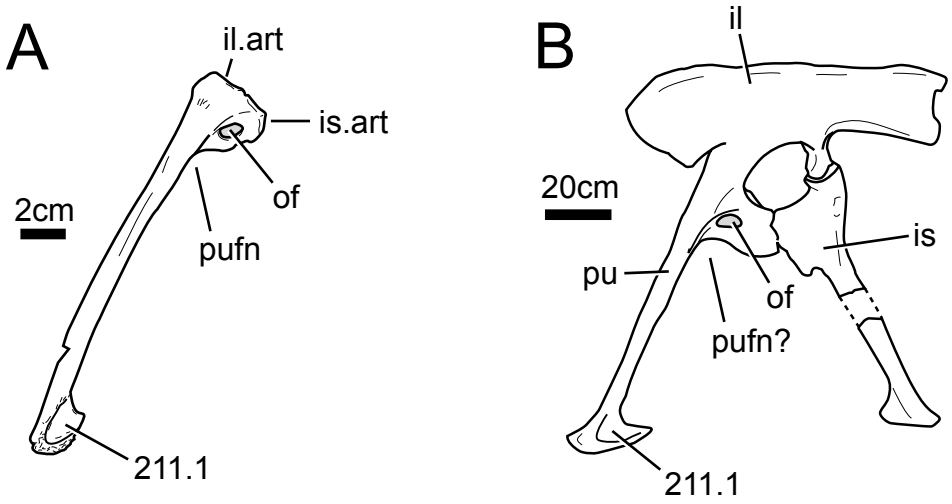


FIGURE 79. Medially inset pubic boot in abelisauroids. A, *Masiakasaurus* (FMNH PR 2108) left pubis, lateral view (after Carrano et al., 2002). B, *Carnotaurus* (MACN-CH 894) left pelvis, lateral view (after Bonaparte et al., 1990).

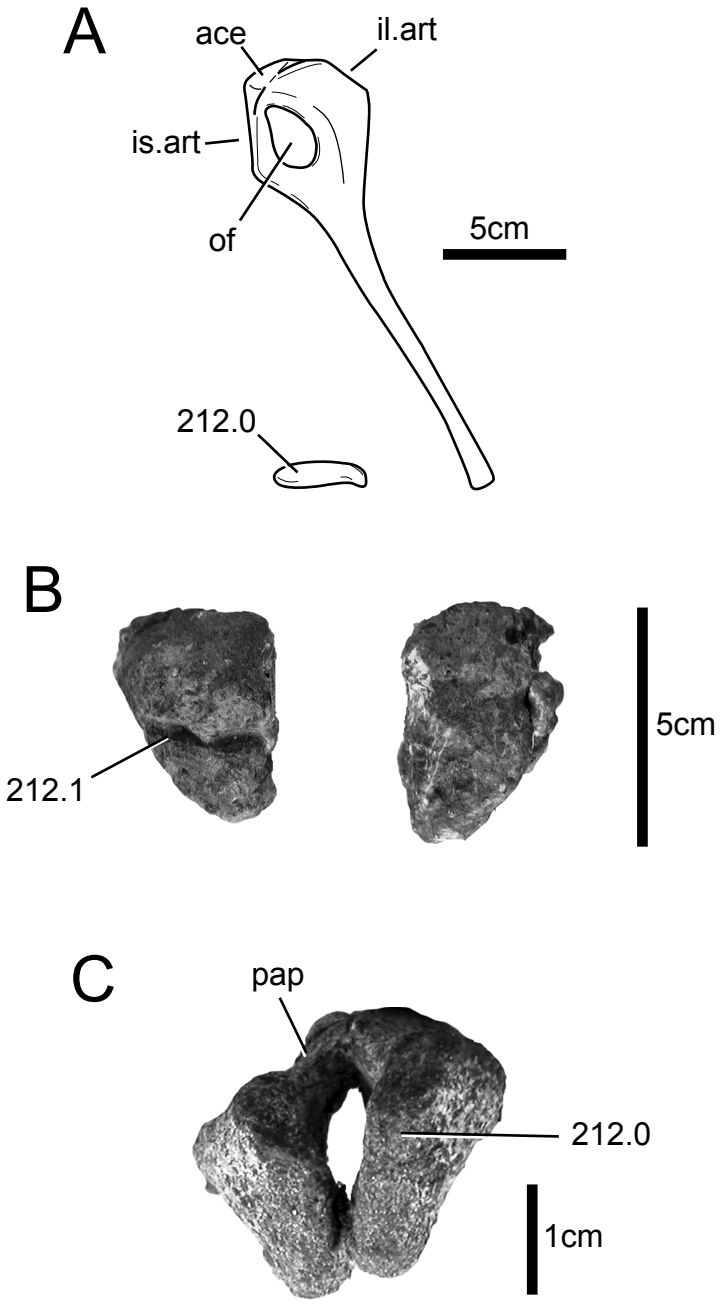


FIGURE 80. Distal pubis profile. A, *Sellosaurus gracilis* (SMNS 12667) right pubis, lateral and distal views (after Galton, 1976). B, *Dilophosaurus* (UCMP 37302) distal pubes, distal view. C, *"Syntarsus" kayentakatae* (MNA V2623) distal pubes, distal view. Anterior to top in all distal views.

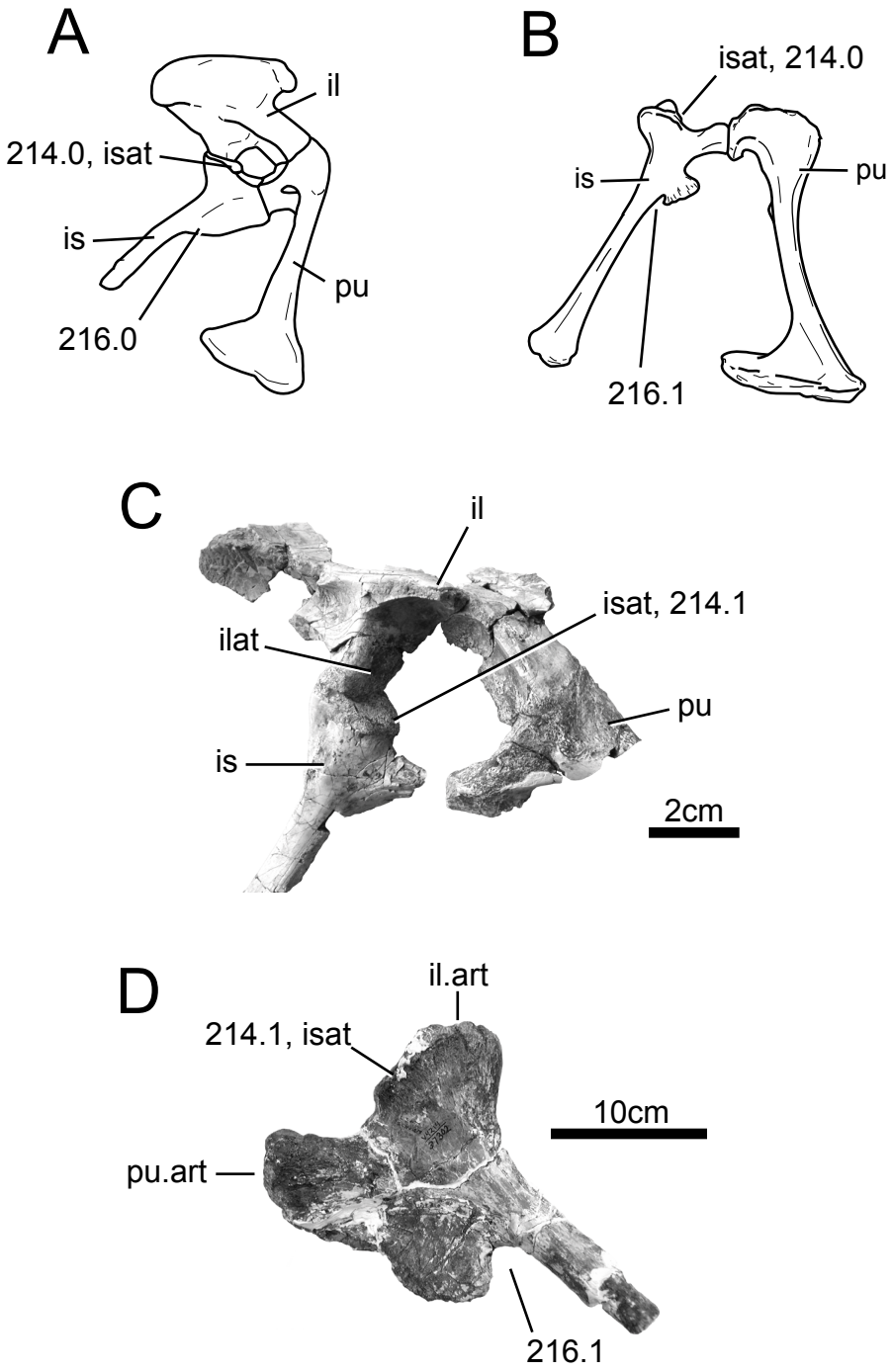


FIGURE 81. Ischial antitrochanter. A, *Herrerasaurus* rightl pelvis, lateral view (after Novas, 1993). B, *Allosaurus* right pubis and ischium, lateral view (after Madsen, 1976). C, *"Syntarsus" kayentakatae* (TMM 43688-1) partial right pelvis, lateral view. D, *Dilophosaurus* (UCMP 37302) left ischium, lateral view.

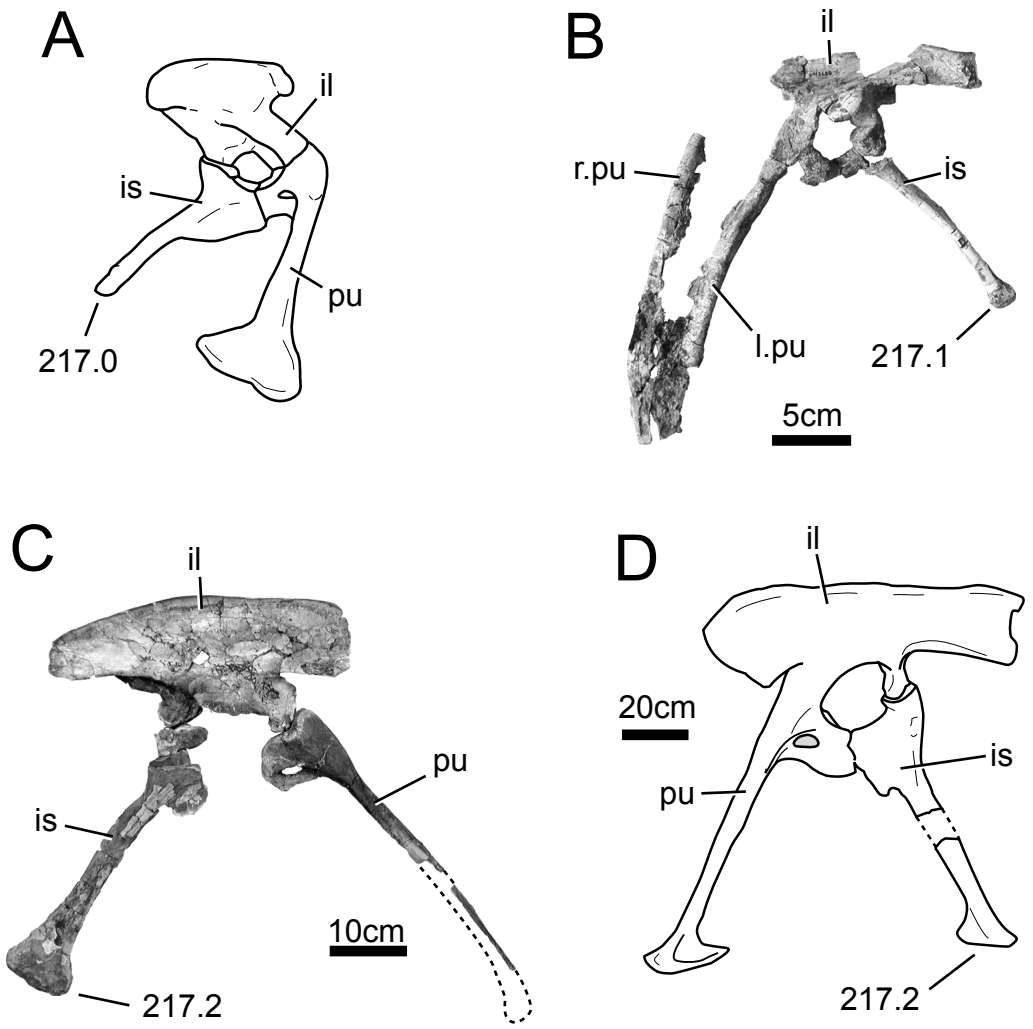


FIGURE 82. Ischium distal expansion. A, *Herrerasaurus* right pelvis, lateral view (after Novas, 1993). B, *"Syntarsus" kayentakatae* (TMM 43688-1) left pelvis and partial right pubic shaft, lateral view. C, *Dilophosaurus* (TMM 43646-26, 43646-33, 43646-59, 43646-79) right ilium, pubis, partial right ischium, partial left ischium, right lateral view. Most of ischial shaft and distal end seen in medial view. D, *Carnotaurus* (MACN-CH 894) left pelvis, lateral view (after Bonaparte et al., 1990).

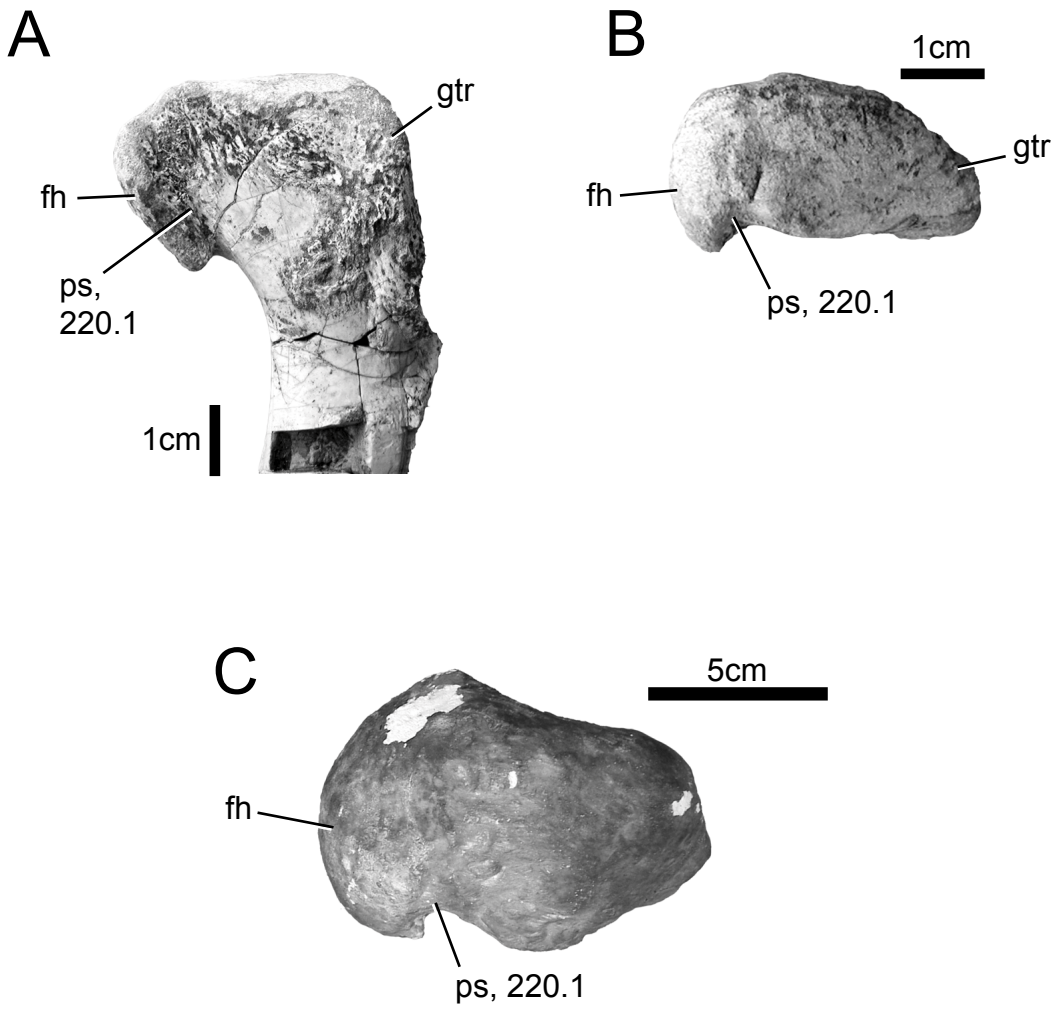


FIGURE 83. Posterior sulcus on the proximal femur. A, *"Syntarsus" kayentakatae* (TMM 43688-1) proximal right femur, posterior view. B, same as in A, proximal view. C, *Xenotarsosaurus* (TMM 45591-1, cast of UNPSJB Pv. 612) right femur, proximal and slightly medial view. Anterior to top in B and C.

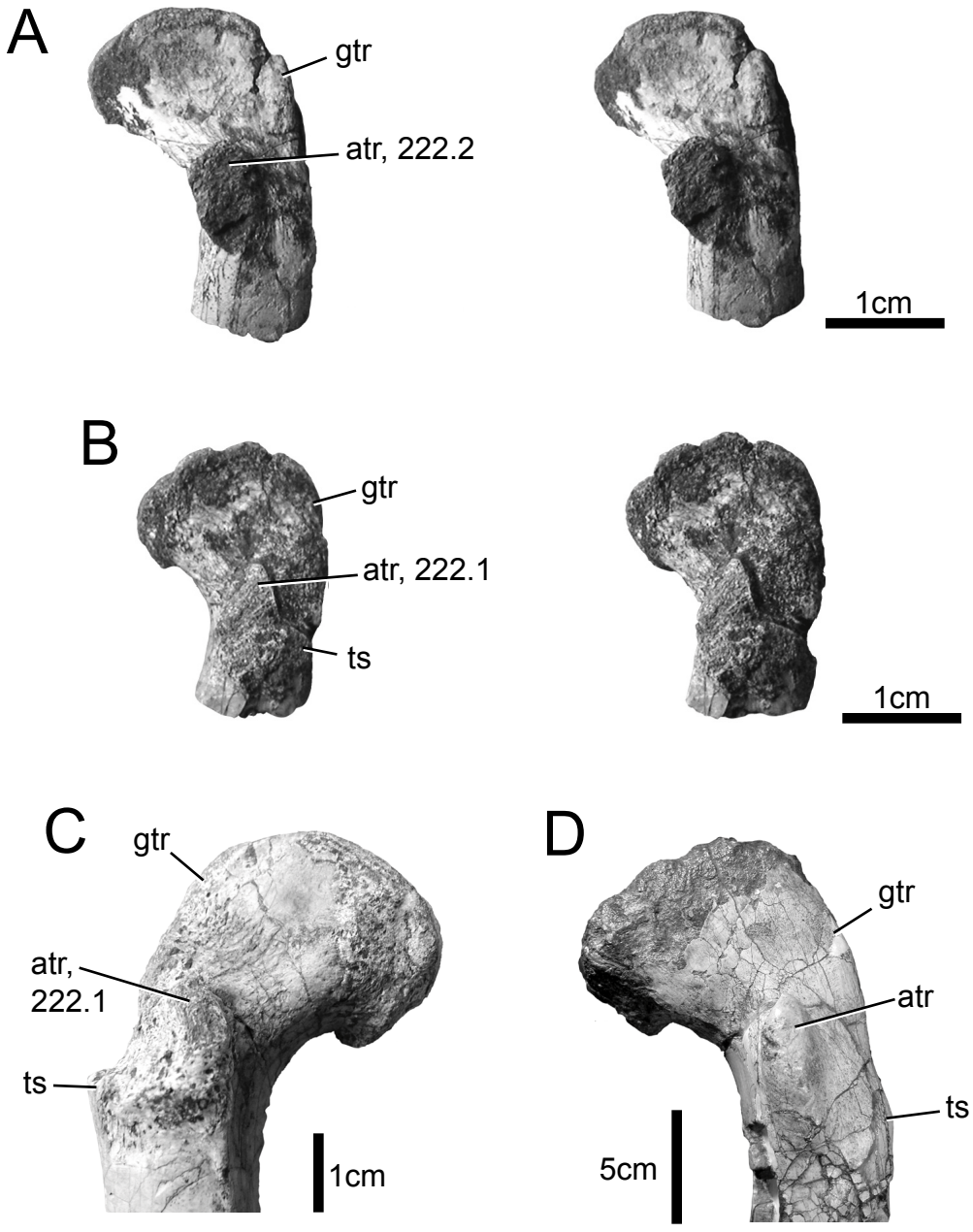


FIGURE 84. Femoral dimorphism in Coelophysoidea. A, Shake-N-Bake taxon (MCZ 9446) stereophotopair of proximal left femur, gracile morphology, anterolateral view. B, Shake-N-Bake taxon (MCZ 9445) stereophotopair of proximal left femur, robust morphology, anterolateral view. C, *"Syntarsus" kayentakatae* (TMM 43688-1) proximal right femur, robust morphology, anterior view. D, *Dilophosaurus* (UCMP 37302) proximal left femur, gracile morphology, anterior view.

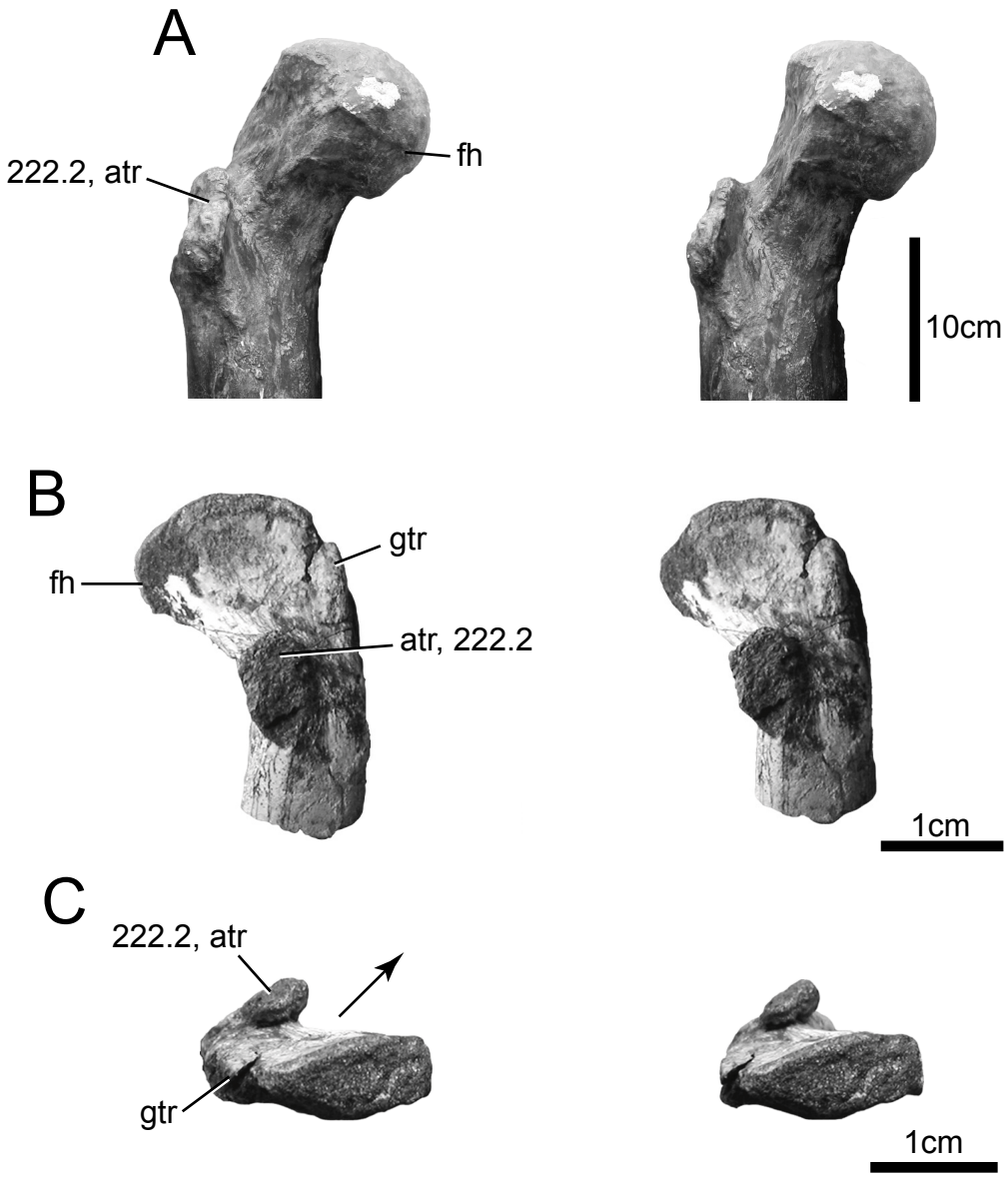


FIGURE 85. 'Wing-like' anterior trochanter . A, *Xenotarsosaurus* (TMM 45591-1, cast of UNPSJB Pv. 612) stereophotopair of proximal right femur, anterior view. B, Shake-N-Bake taxon (MCZ 9446) stereophotopair of proximal left femur, anterolateral view. C, Shake-N-Bake taxon (MCZ 9446) stereophotopair of proximal left femur, proximal view. Anterior direction in C shown by arrow.

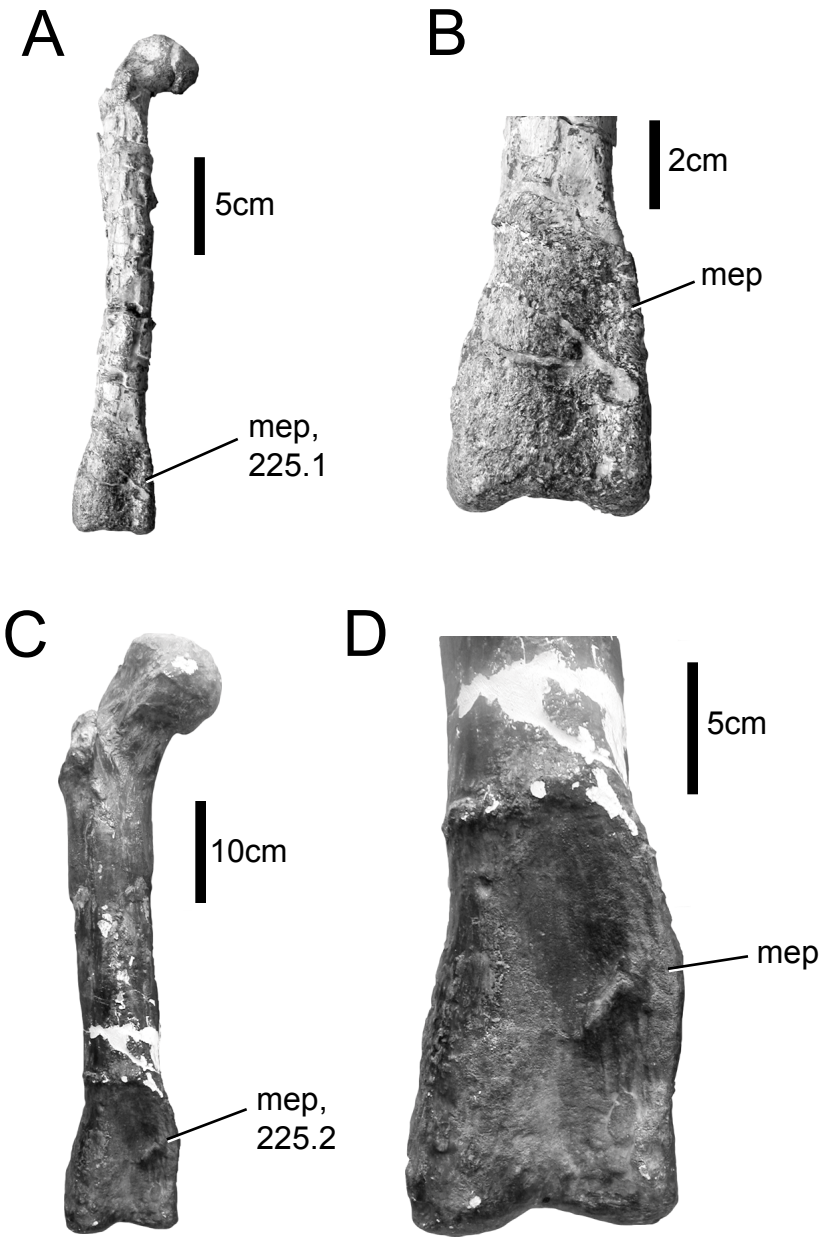


FIGURE 86. Medial epicondyle development. A, *"Syntarsus" kayentakatae* (MNA V 2623) right femur, anterior view. B, same as in A, close-up of medial epicondyle on distal femur, anterior view. C, *Xenotarsosaurus* (TMM 45591-1) right femur, anterior view. D, same as in C, close-up of medial epicondyle on distal femur, anterior view.

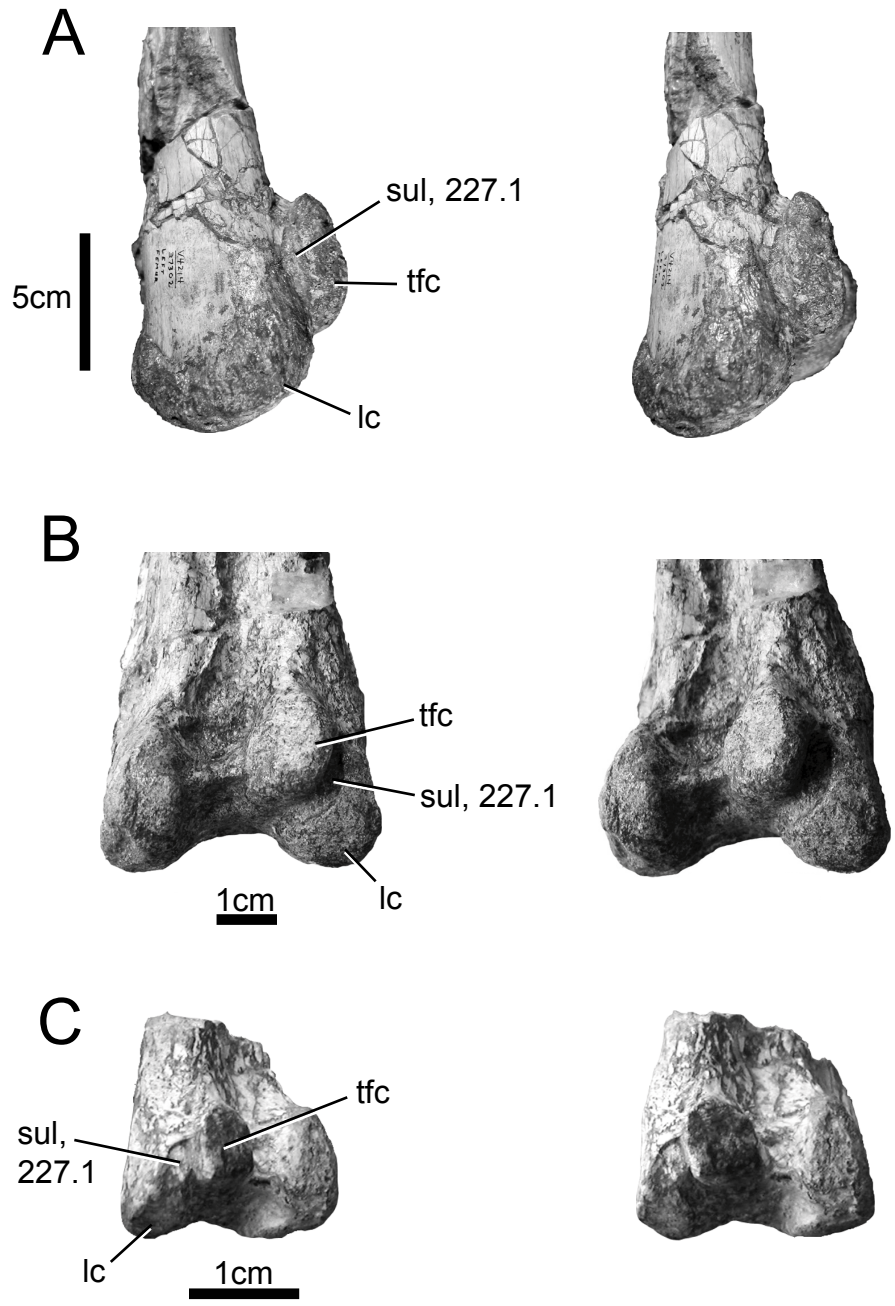


FIGURE 87. Tibiofibular crest lateral sulcus. A, *Dilophosaurus* (UCMP 37302) stereophotopair of left femur distal end, lateral view. B, *"Syntarsus" kayentakatae* (MNA V2623) stereophotopair of right femur distal end, posterior view. C, *Coelophysis* (TMM 45559-15) stereophotopair of left femur distal end, postero-lateral view.

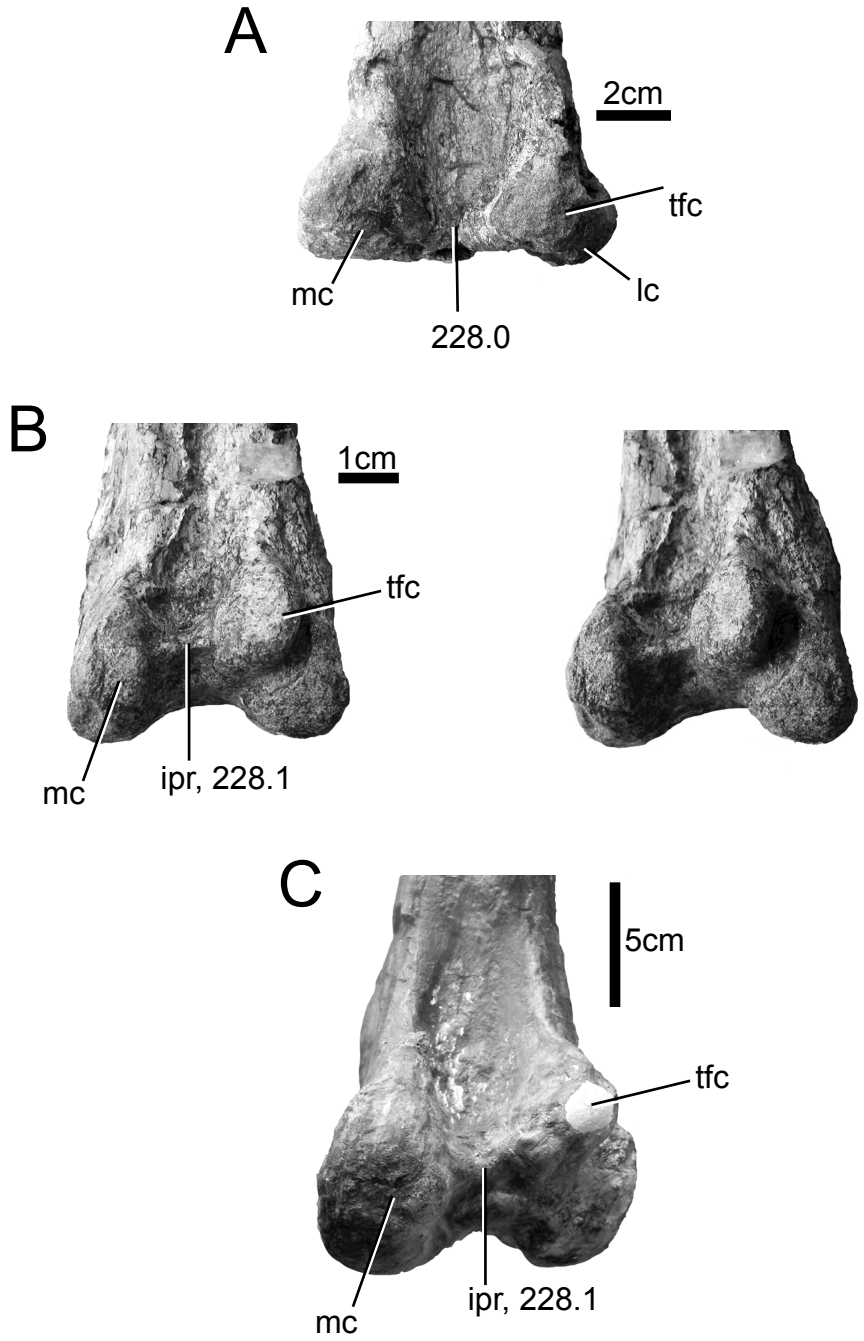


FIGURE 88. Infrapopliteal ridge on distal femur. A, Kayenta Formation prosauropod (TMM 43646-43) right femur distal end, posterior view. B, *"Syntarsus" kayentakatae* (MNA V2623) stereophotopair of right femur distal end, posterior view. C, *Xenotarsosaurus* (TMM 45591-1) cast of right femur distal end, posterior view.

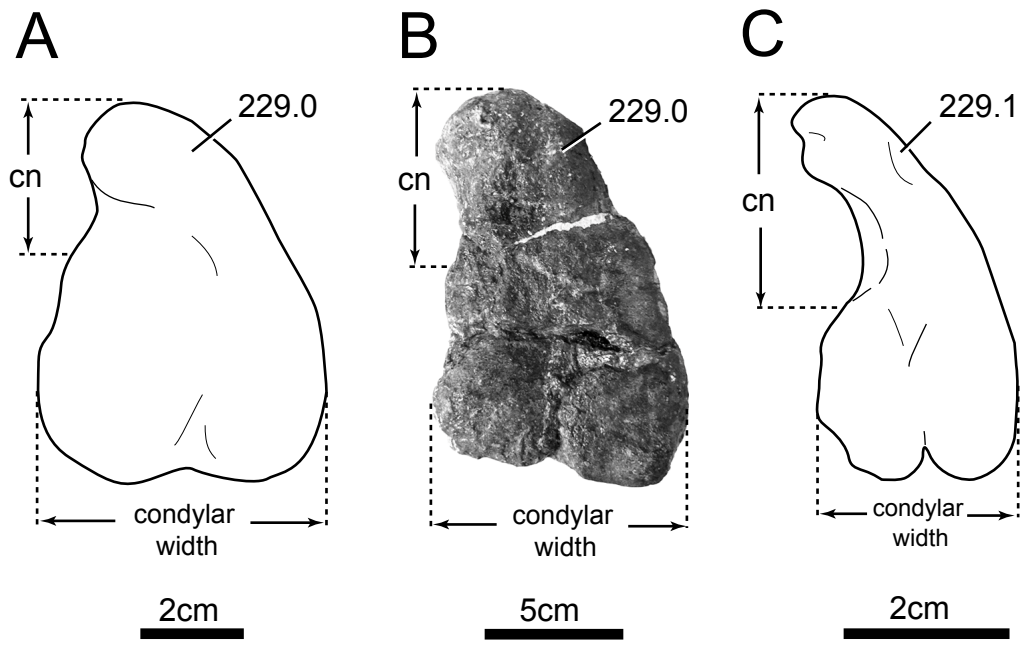


FIGURE 89. Cnemial crest relative size. A, *Herrerasaurus* (PVSJ 373) left tibia, proximal view (after Novas, 1993). B, *Dilophosaurus* (UCMP 37302) left tibia, proximal view. C, *Masiakasaurus* (FMNH PR 2118) left tibia, proximal view (after Carrano et al., 2002).

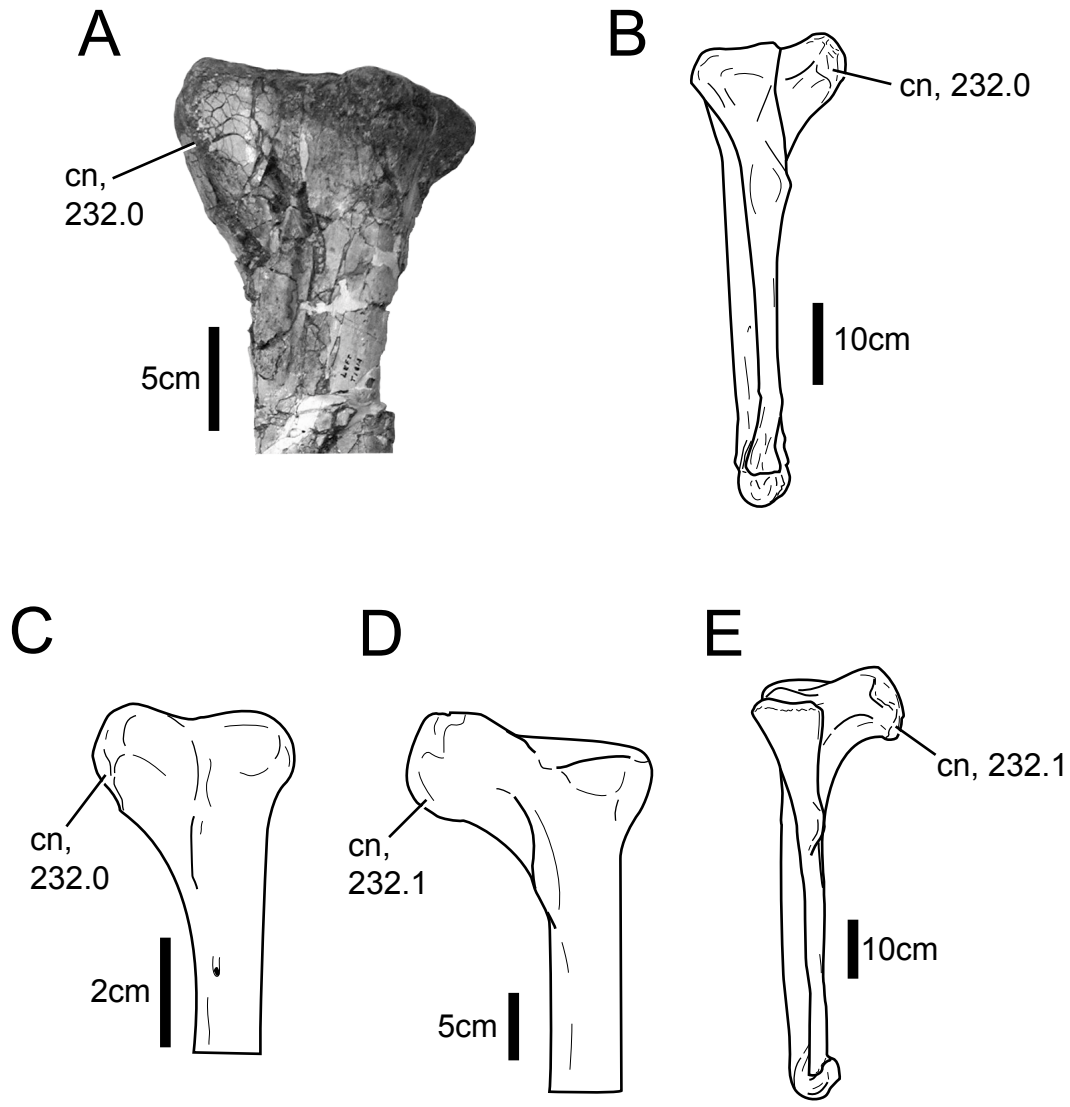


FIGURE 90. Cnemial crest dorsoventral expansion. A, *Dilophosaurus* (UCMP 37302) left proximal tibia, lateral view. B, *Ceratosaurus* (USNM 4735) right fibula and tibiotarsus, lateral view (after Gilmore, 1920). C, *Masiaksasaurus* (FMNH PR 2118) left proximal tibia, lateral view (after Carrano et al., 2002). D, *Majungatholus* proximal left tibia, lateral view (after Rauhut, 2003; based upon FMNH/UA 95263). E, *Aucasaurus* (MCF-PVPH-236) right fibula and tibiotarsus, lateral view (after Coria et al., 2002)

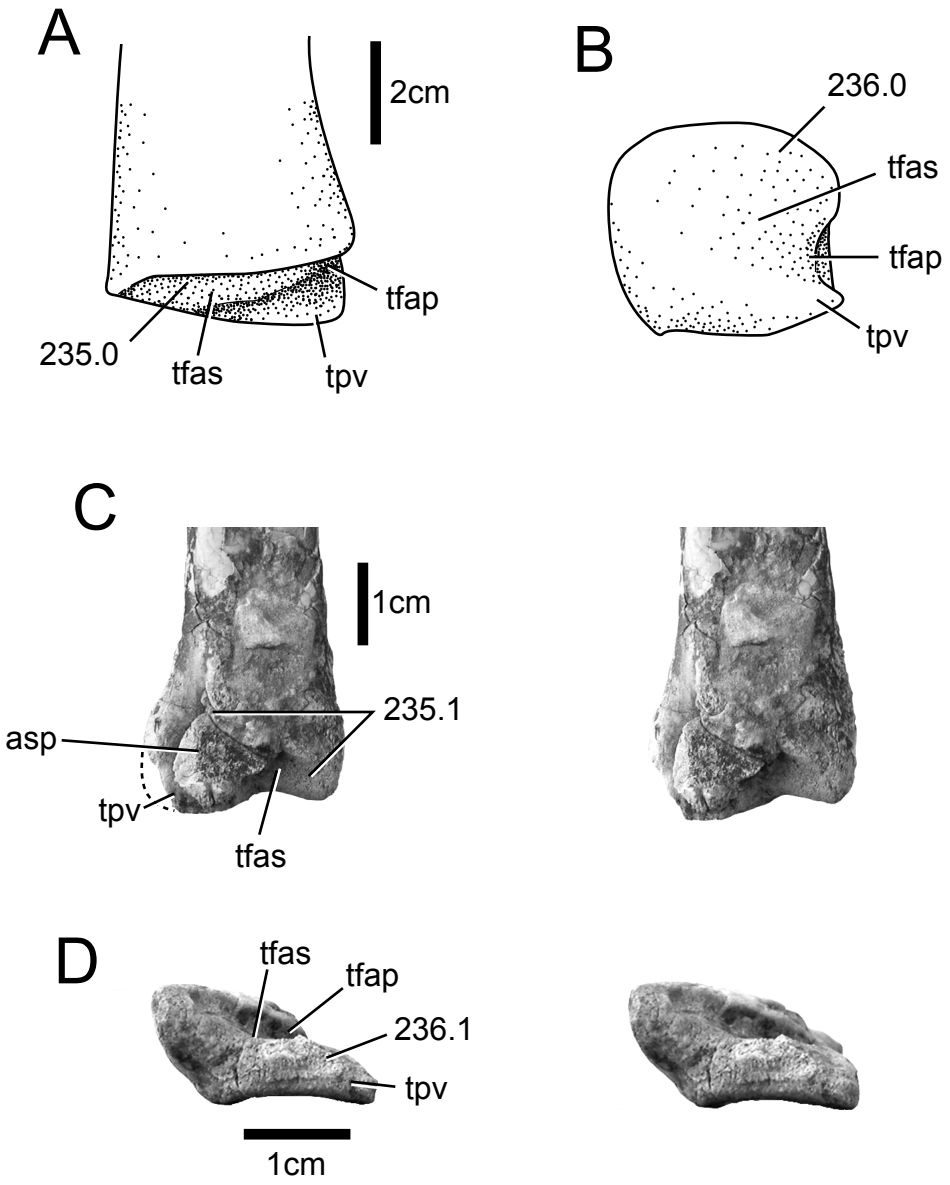


FIGURE 91. Fossa on distal tibia for ascending process of astragalus. A, *Herrerasaurus* (PVSJ 373) distal tibia, anterior view (after Novas, 1993). B, same as in A, distal view. C, *"Syntarsus" kayentakatae* (TMM 43669-3) stereophotopair of distal right tibia and ascending process of astragalus, anterior view. D, *"Syntarsus" kayentakatae* (TMM 43669-3) stereophotopair of distal left tibia, distal view.

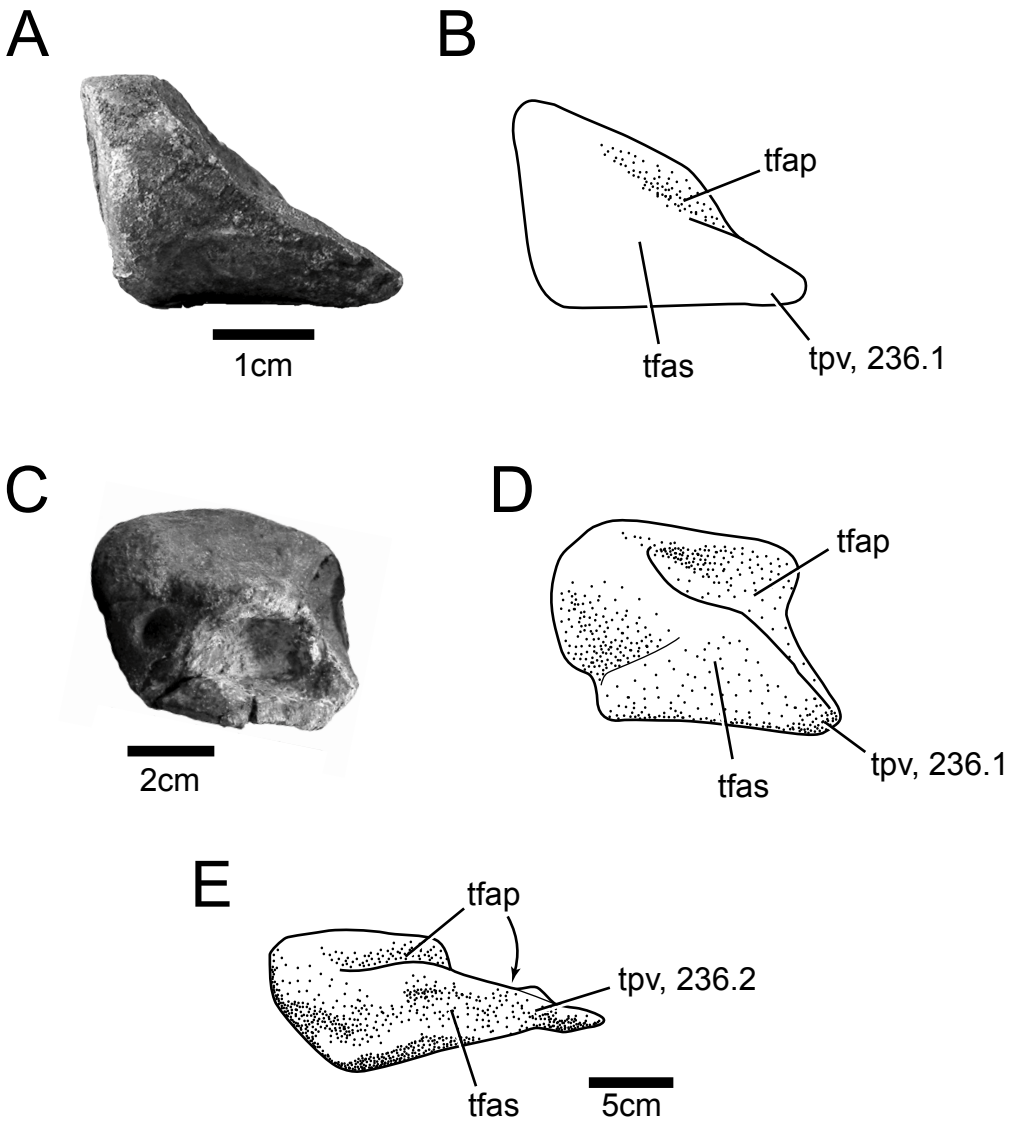


FIGURE 92. Distal tibia profile. A, *"Syntarsus" kayentakatae* (TMM 43658-9) partial left tibiotarsus missing most of astragalocalcaneum. Much of the tibia's posteroventral process is exposed. B, Reconstruction of the distal profile of the left tibia of "*Syntarsus*" *kayentakatae*, based upon MNA V2623, TMM 43648-9, and TMM 43669-3. C, *Dilophosaurus* (TMM 43646-78) left tibia, distal view. D, Reconstruction of *Dilophosaurus* distal tibia profile based upon UCMP 37302, observations of UCMP 77270, and TMM 43646-78. E, *Torvosaurus* (BYUVP 2016) right tibia (reversed for easy comparison to A-D), distal view (after Britt, 1991).

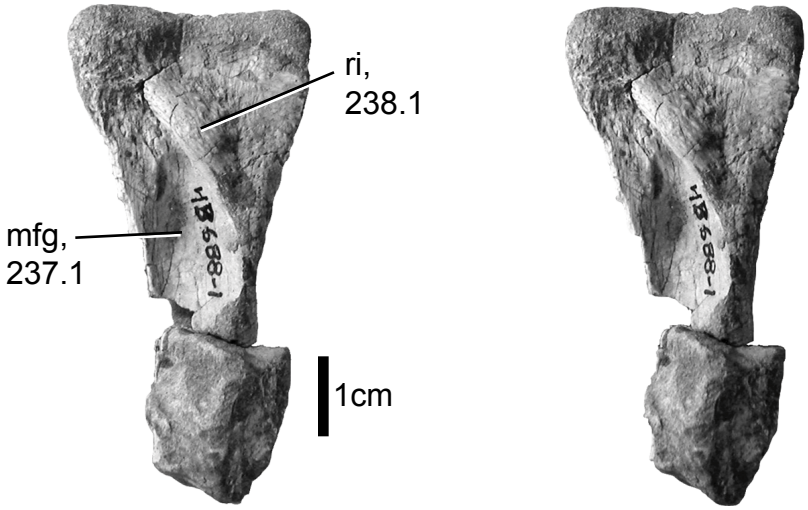


FIGURE 93. *"Syntarsus" kayentakatae* (TMM 43688-1) proximal fibula. Stereophotopair of partial left proximal fibula, medial view. Medial fibular groove and oblique ridge overlapping the groove's proximal end are clearly visibile.

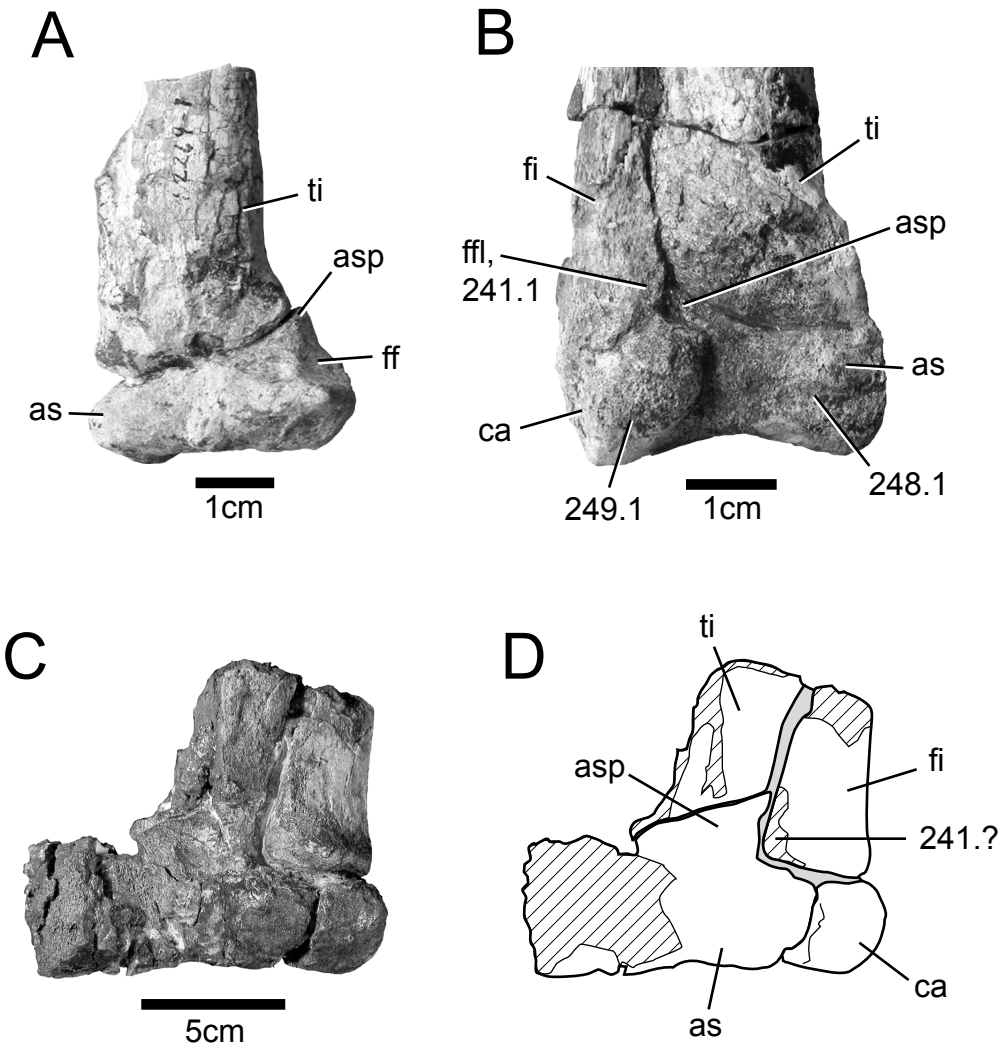


FIGURE 94. Distal fibula with anterolateral flange. A, prosauropod (TMM 42269-1) distal tibia and astragalus. B, *"Syntarsus" kayentakatae* (MNA V2623) right distal tibiarsus in anterior view. C, *Dilophosaurus* (UCMP 37303) partial left tibia, fibula, astragalus, and calcaneum in articulation, anterior view. D, line drawing of C showing elements. Gray fill indicates sediment. Cross-hatching indicates broken or eroded bone surfaces.

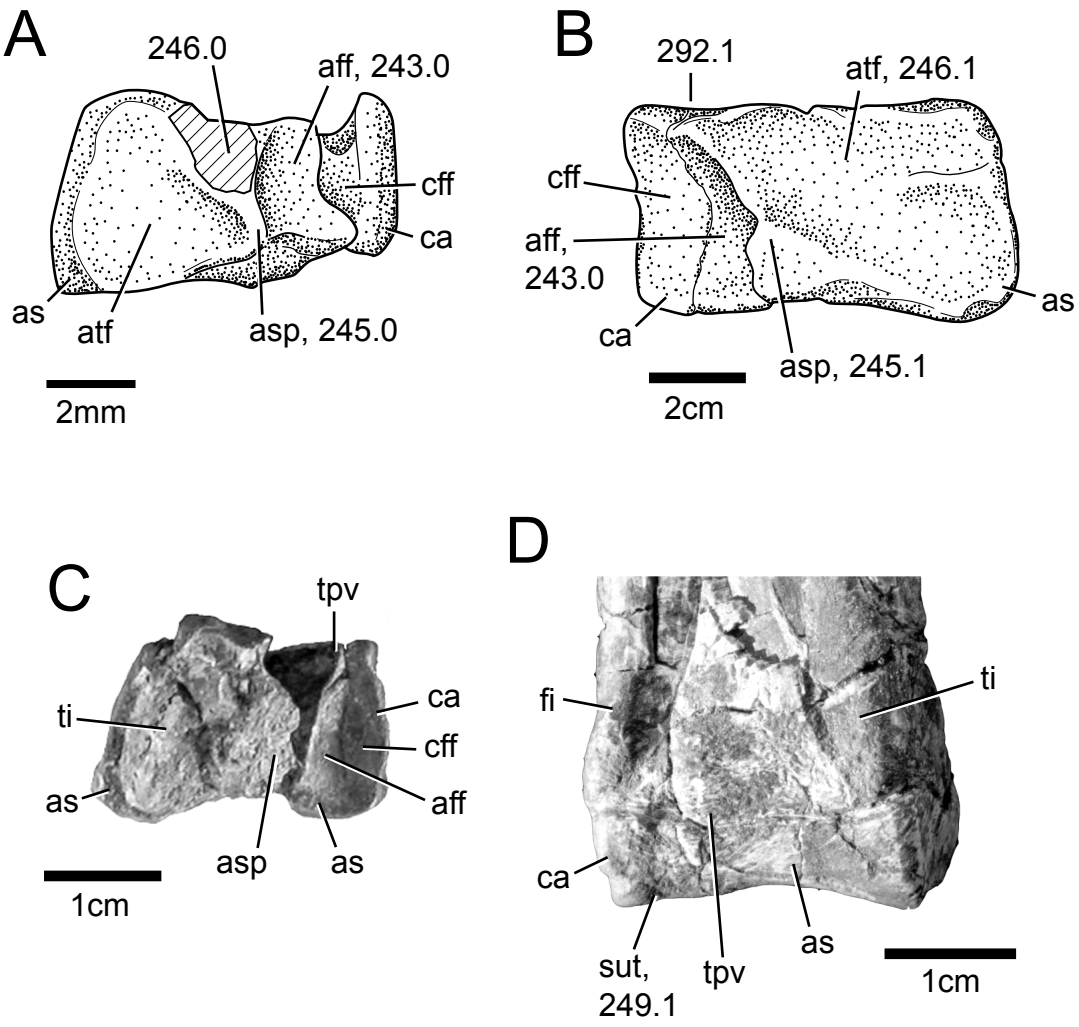


FIGURE 95. Astragalus and calcaneum proximal surfaces. A, *Marasuchus* (PVL 3870) left astragalus and calcaneum, proximal view (after Sereno and Arcucci, 1994). B, *Liliensternus* (MB R.2175.14) right astragalocalcaneum, proximal view. C, *Coelophysis* (TMM 45559-16) left distal tibia and astragalocalcaneum, proximal view. D, *Coelophysis* (CMNH 11894) left distal tibia, fibula, and astragalocalcaneum, posterior view. A-C, anterior to bottom.

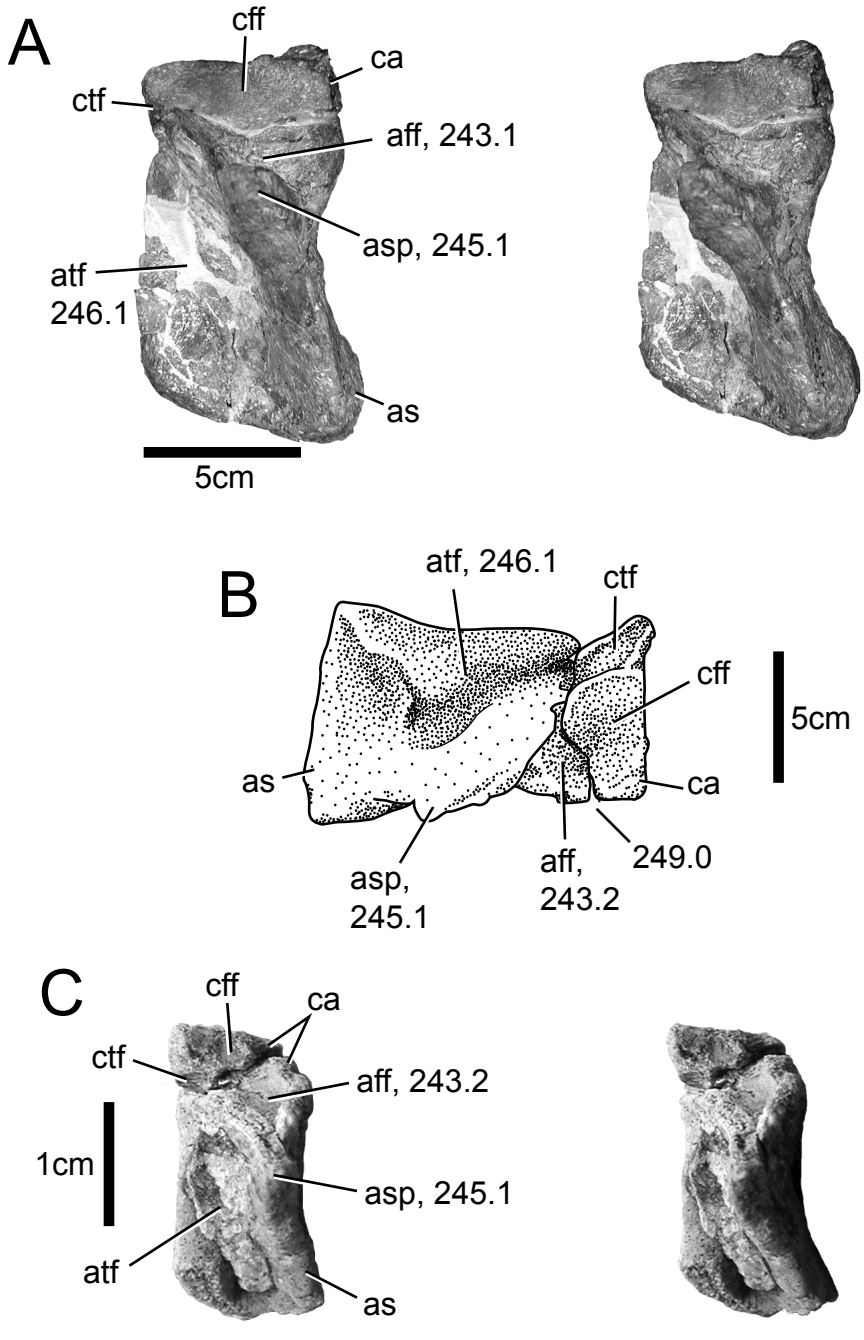


FIGURE 96. Astragalus and calcaneum proximal surfaces. A, *Dilophosaurus* (UCMP 37302) stereophotopair of left astragalus and calcaneum, proximal view. B, *Allosaurus* (MOR 693) left astragalus and calcaneum, proximal and slightly posterior view (after Rauhut, 2003). C, *"Syntarsus" kayentakatae* (TMM 43669-3) stereophotopair of left astragalus and calcaneum, proximal view.

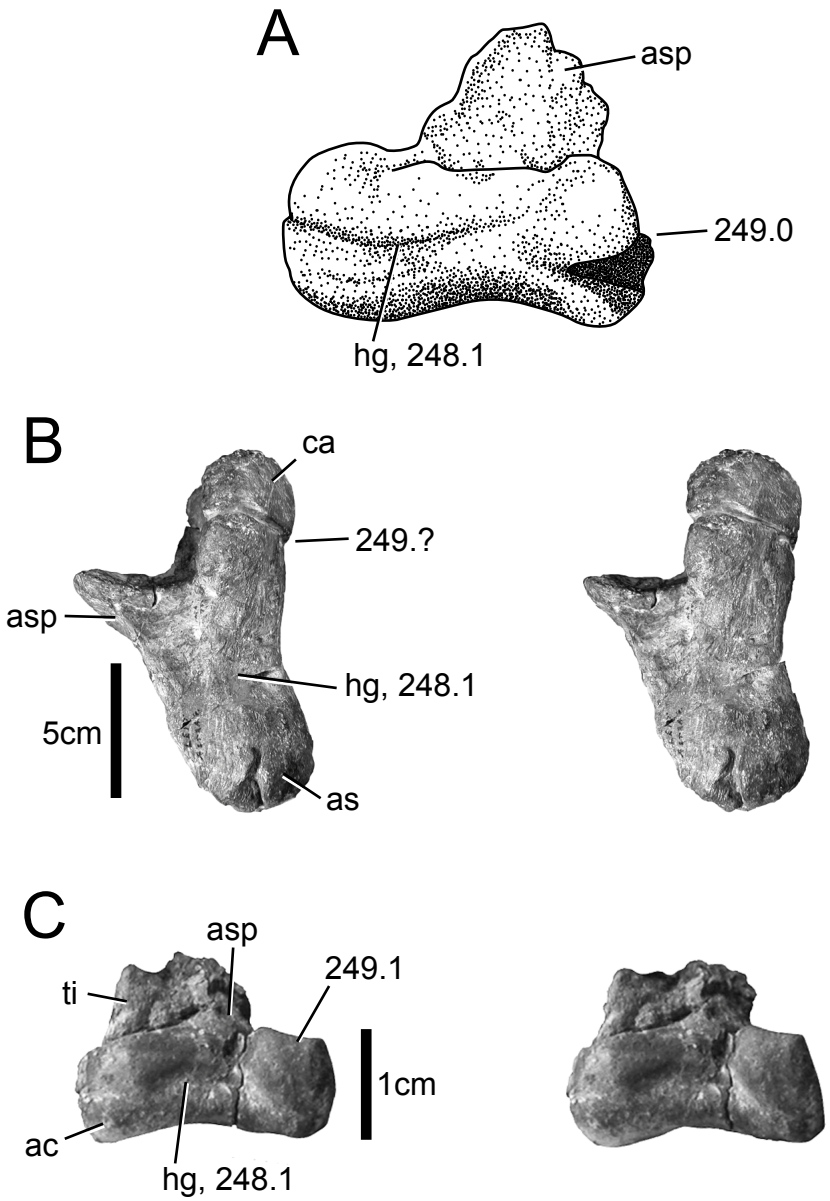


FIGURE 97. Horizontal groove on anterior surface of astragalus. A, *Allosaurus* (USNM 7336) left astragalus, anterior view (after Gilmore, 1920). B, *Dilophosaurus* (UCMP 37302) stereophotopair of left astragalus and calcaneum, anterior view. Lateral to top. C, *Coelophysis* (TMM 45559-16) stereophotopair of left distal tibia and astragalocalcaneum, anterior view.

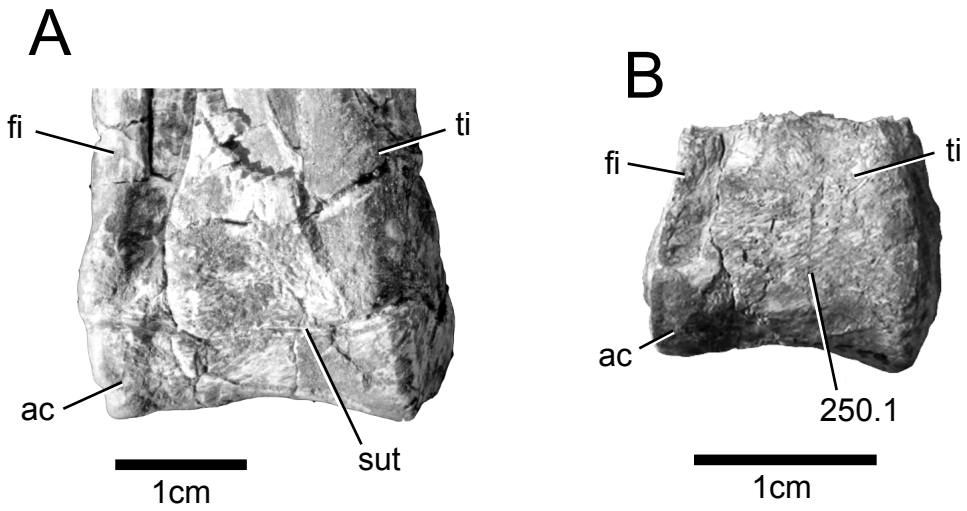


FIGURE 98. Tibia-tarsal fusion in *Coelophysis*. A, *Coelophysis* (CMNH 11894) distal left tibia, fibula, and astragalocalcaneum, posterior view. No co-ossification between tibia and proximal tarsals. B, *Coelophysis* (TMM 45559-14), distal left tibiotarsus and fibula, posterior view. Complete fusion present between tibia and proximal tarsals.

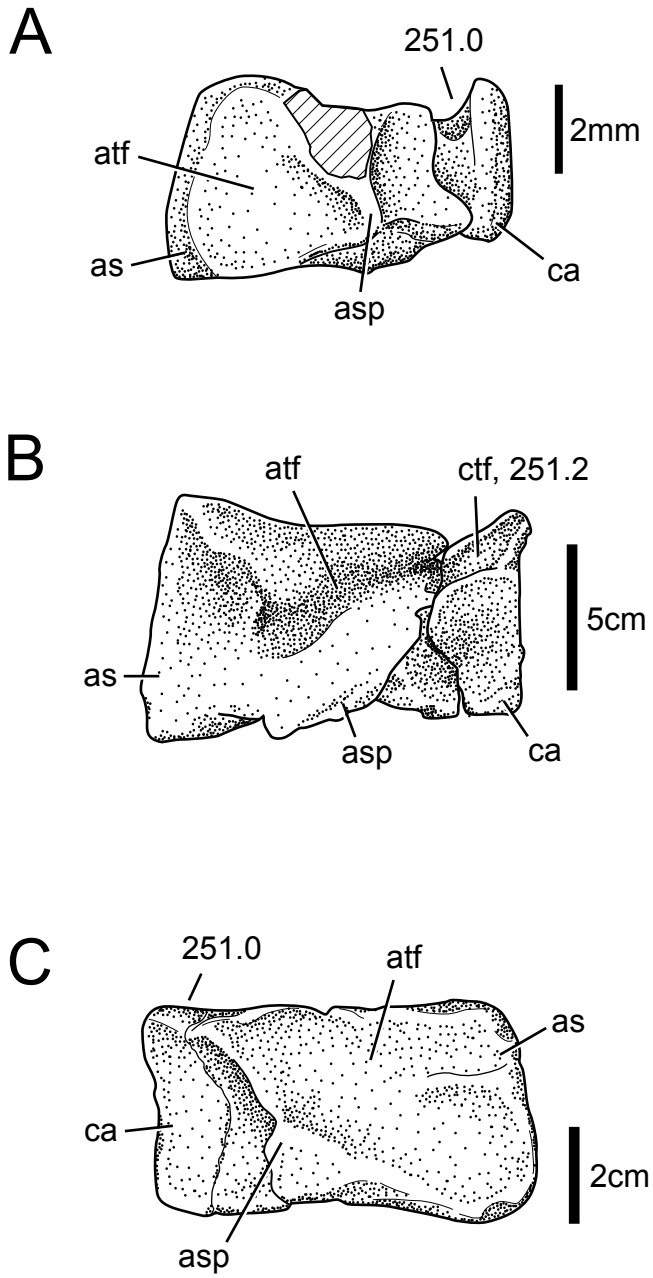


FIGURE 99. Tibia-calcaneum contact. A, *Marasuchus* (PVL 3870) left astragalus and calcaneum, proximal view (after Sereno and Arcucci, 1994). B, *Allosaurus* (MOR 693) left astragalus and calcaneum, proximal view (after Rauhut, 2003). C, *Liliensternus* (MB R. 2175.14) right astragalocalcaneum, proximal view.

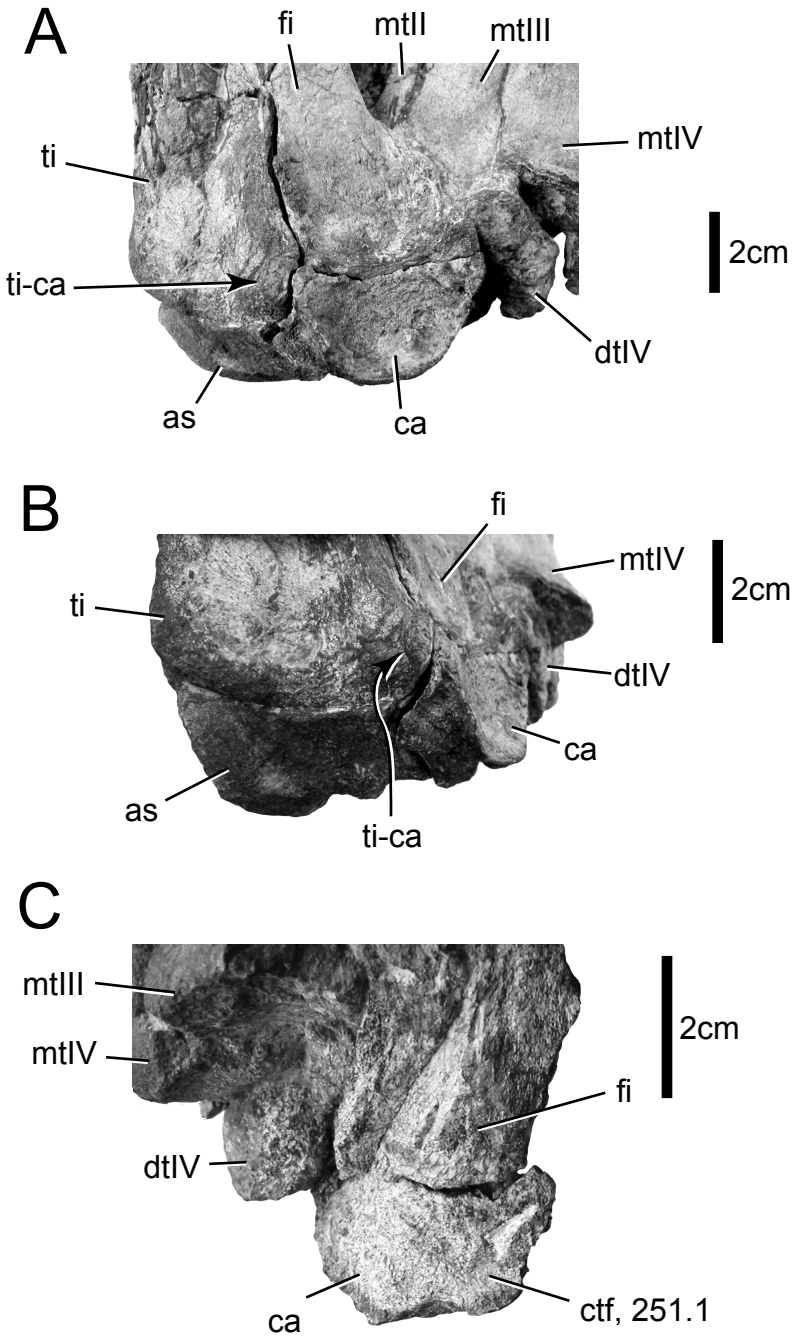


FIGURE 100. Tibia-calcaneum contact in *Dilophosaurus*. TMM 43646-61, right tibia, fibula, proximal and distal tarsals, and metatarsals in A, posterolateral, and B, posterior and slightly lateral views. C, part of same specimen removed along large break, showing calcaneum tibial facet (ctf), medial view. Arrows point to tibia-calcaneum contact in A and B.

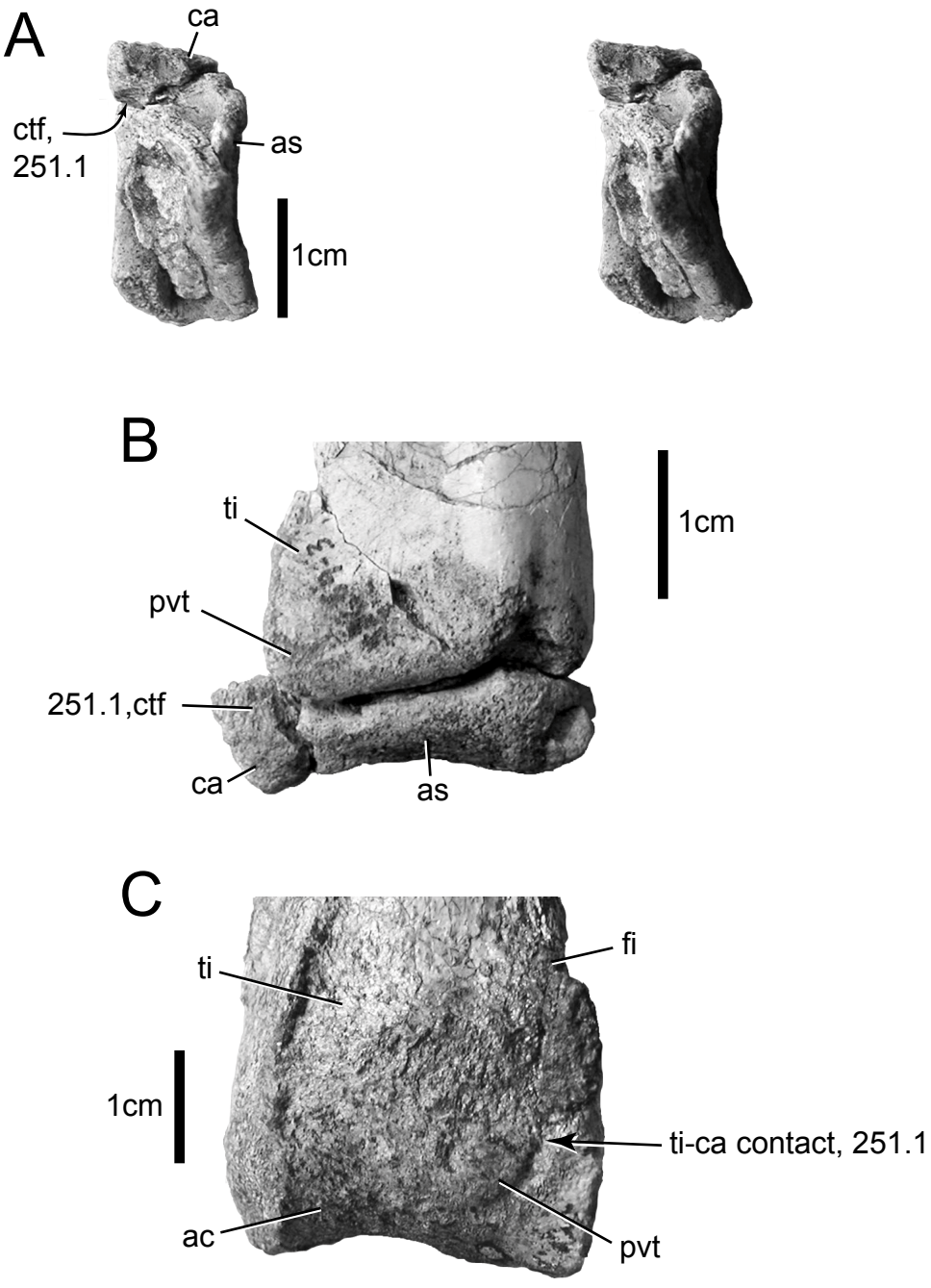


FIGURE 101. Tibia-calcaneum contact in *"Syntarsus" kayentakatae*. A, TMM 43669-3 stereophotopair of left astragalus and calcaneum, proximal view. B, TMM 43669-3 left distal tibia, astragalus, and calcaneum, posterior view. C, MNA V2623 distal right tibiotarsus and fibula, posterior view.

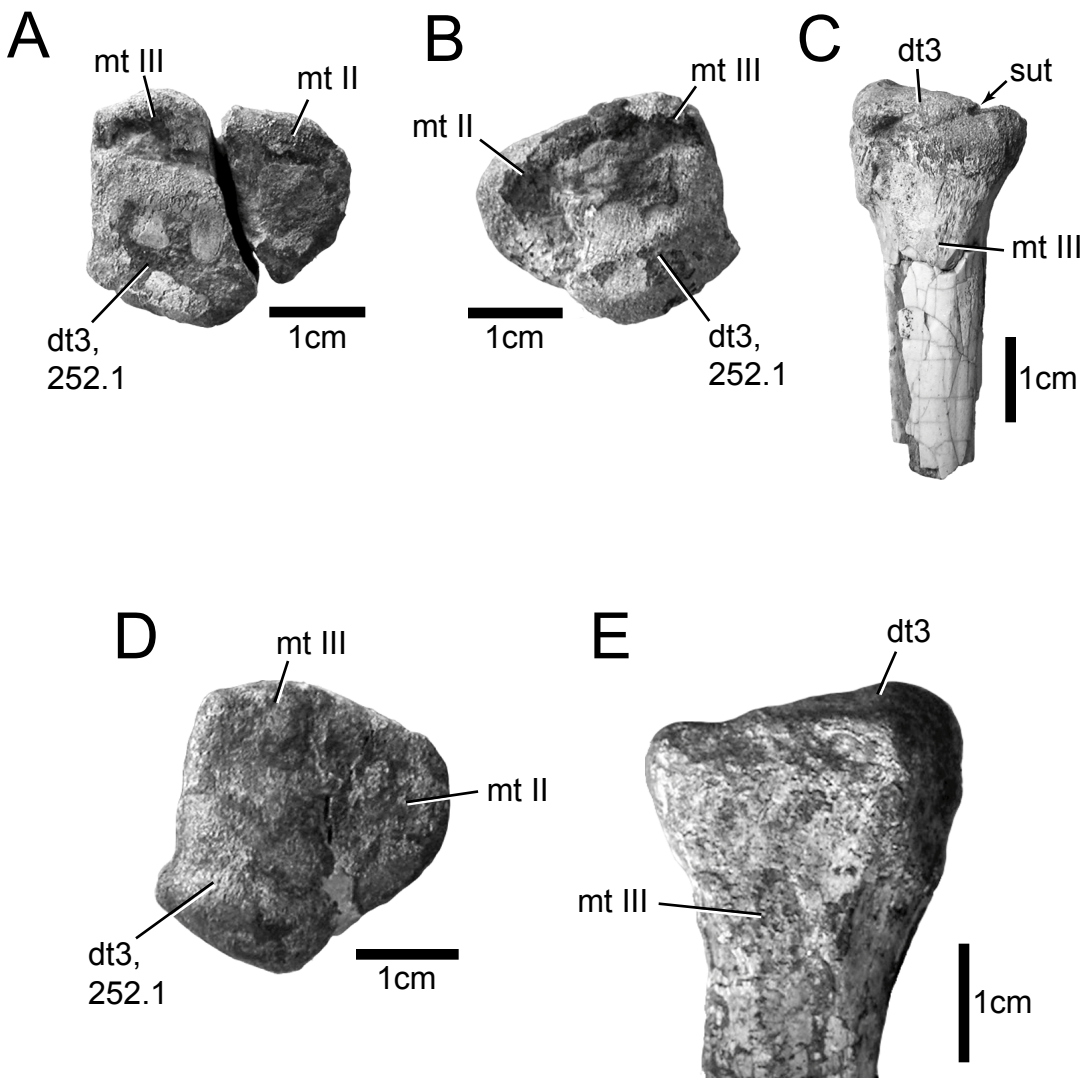


FIGURE 102. Distal tarsal 3-metatarsal III coossification. A, *"Syntarsus" kayentakatae* (TMM 43688-1) left metatarsal II, distal tarsal 3, and metatarsal III, proximal view. B, same individual, right tarsometatarsus (mt II, dt3, mt III), proximal view. C, same as in B, lateral view. Suture between distal tarsal 3 and metatarsal III is visible. D, *"Syntarsus" kayentakatae* (MNA V2623) left tarsometatarsus, proximal view. E, same as D, lateral view. Note, there is complete fusion between distal tarsal 3 and metatarsal III.

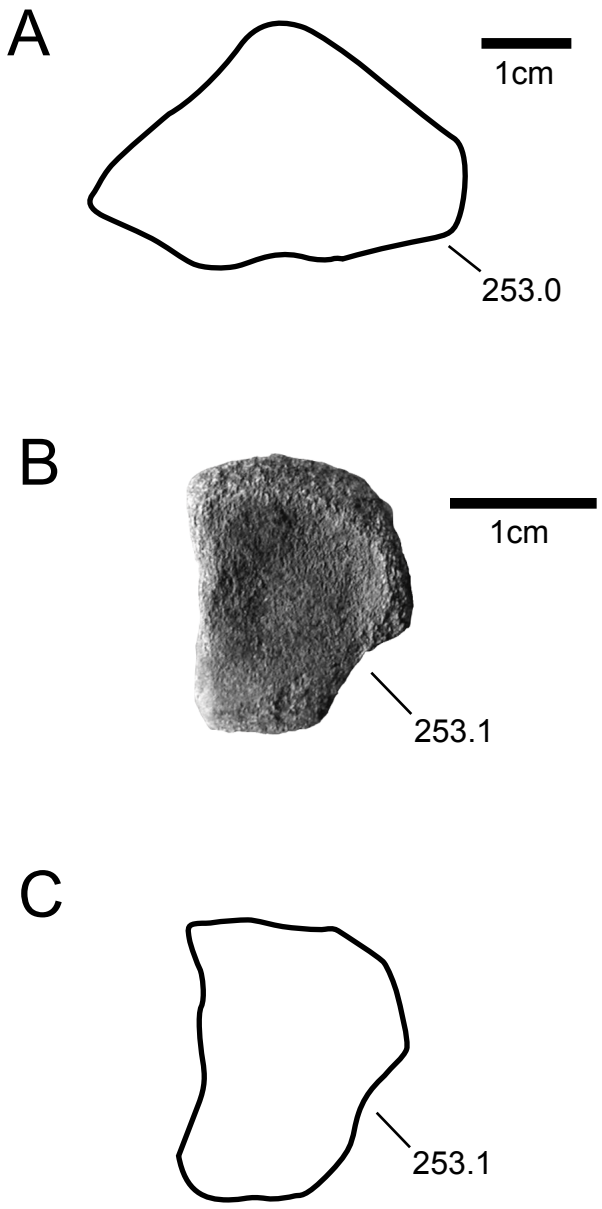


FIGURE 103. Distal tarsal 4. A, *Herrerasaurus* (PVSJ 373) right distal tarsal 4 profile in proximal view (after Novas, 1993). B, *"Syntarsus" kayentakatae* (TMM 43688-1) right distal tarsal 4, proximal view. C, *Allosaurus* right distal tarsal 4, proximal view (reversed from left distal tarsal 4 illustrated by Madsen, 1976). Anterior to top in all three examples.

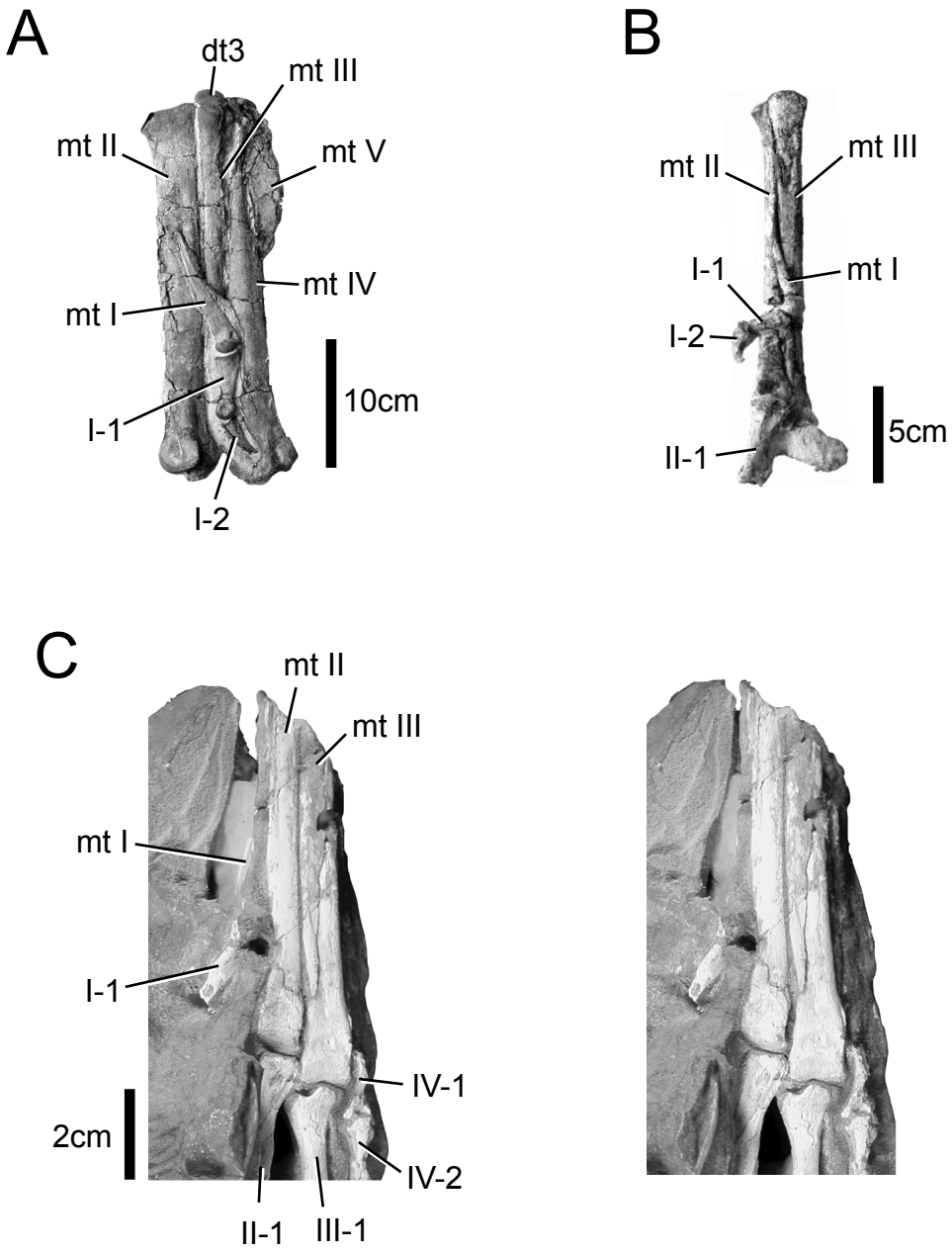


FIGURE 104. Pedal digit I position in coelophysoid theropods. A, *Dilophosaurus* (TMM 43646-61) right metatarsals I-V, ventral/plantar view. B, *"Syntarsus" kayentakatae* (MNA V2623) right digit I, tarsometatarsus (mt II + dt3 + mt III), ventral/plantar view. C, *Segisaurus* (UCMP 32101) stereophotopair of parts of left pes in anterior and slightly medial view.

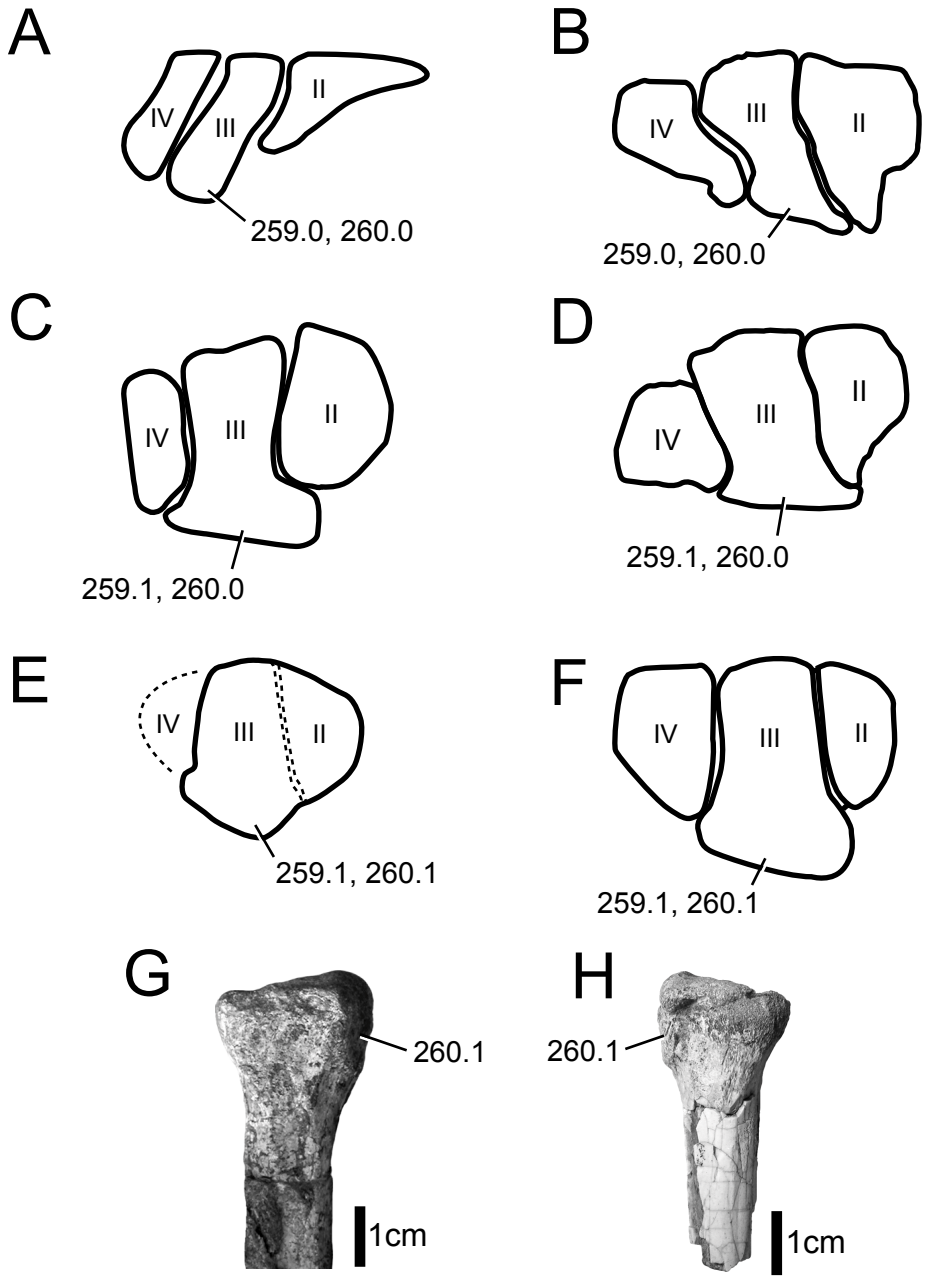


FIGURE 105. Metatarsal III ventral/posterior expansion. Proximal outlines of left metatarsals II-IV. A, *Herrerasaurus* (PVL 2556; after Novas, 1993). B, *Allosaurus* (after Madsen, 1976). C, *Elaphrosaurus* (after Janensch, 1925). D, *Ceratosaurus* (USNM 4735; after Gilmore, 1920). E, *"Syntarsus" kayentakatae* (MNA V2623). F, *Syntarsus rhodesiensis* (QG 768; after Raath, 1977). Anterior to top. Not to scale. G, *"Syntarsus" kayentakatae* (MNA V2623) proximal left tarsometatarsus, lateral view. H, *"Syntarsus" kayentakatae* (TMM 43688-1) partial proximal right tarsometatarsus, lateral view.

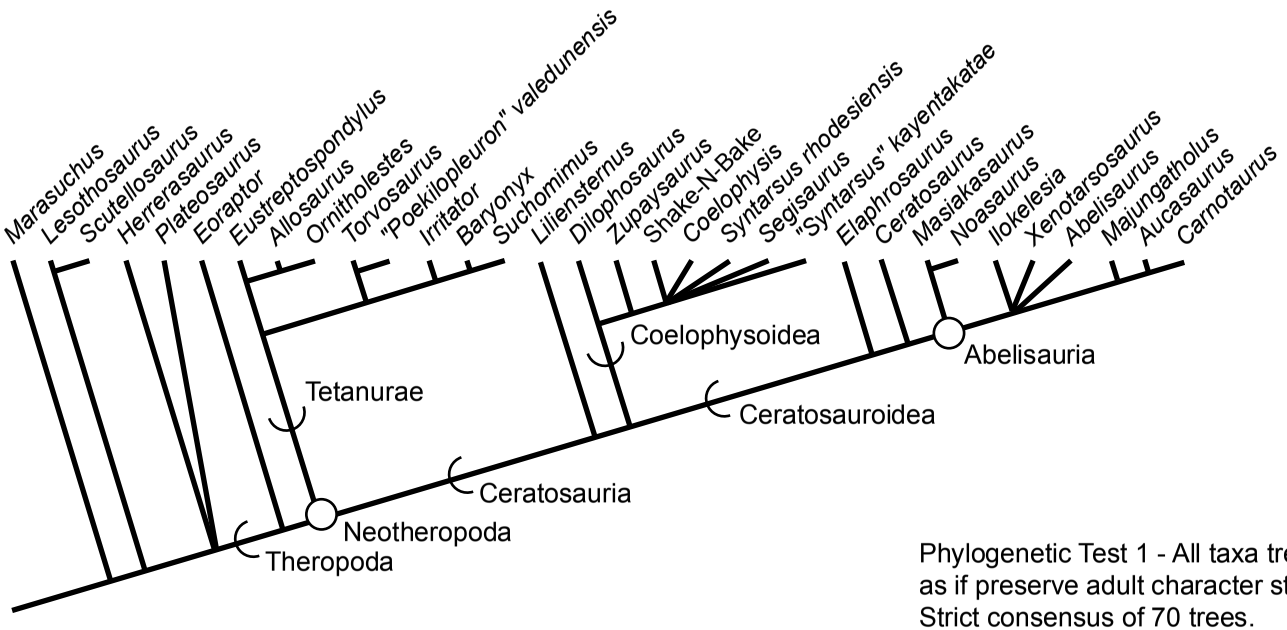


FIGURE 106A. Phylogenetic Test 1. Strict consensus tree of 70 equally most parsimonious hypotheses of basal theropod phylogeny. All taxa were scored as if they were known from adult specimens. Length = 619, C.I.=0.4895, R.I.=0.7288. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

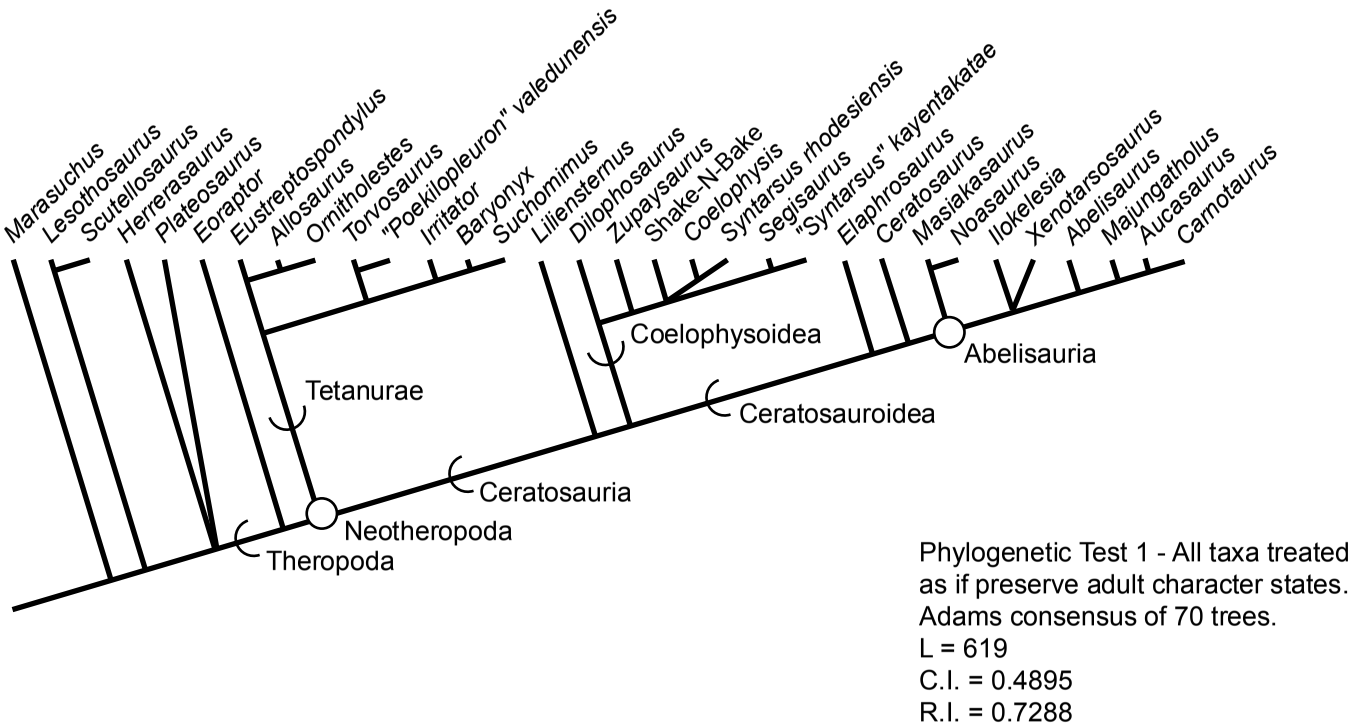


FIGURE 106B. Phylogenetic Test 1. Adams consensus tree of 70 equally most parsimonious hypotheses of basal theropod phylogeny. All taxa were scored as if they were known from adult specimens. Length = 619, C.I.=0.4895, R.I.=0.7288. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

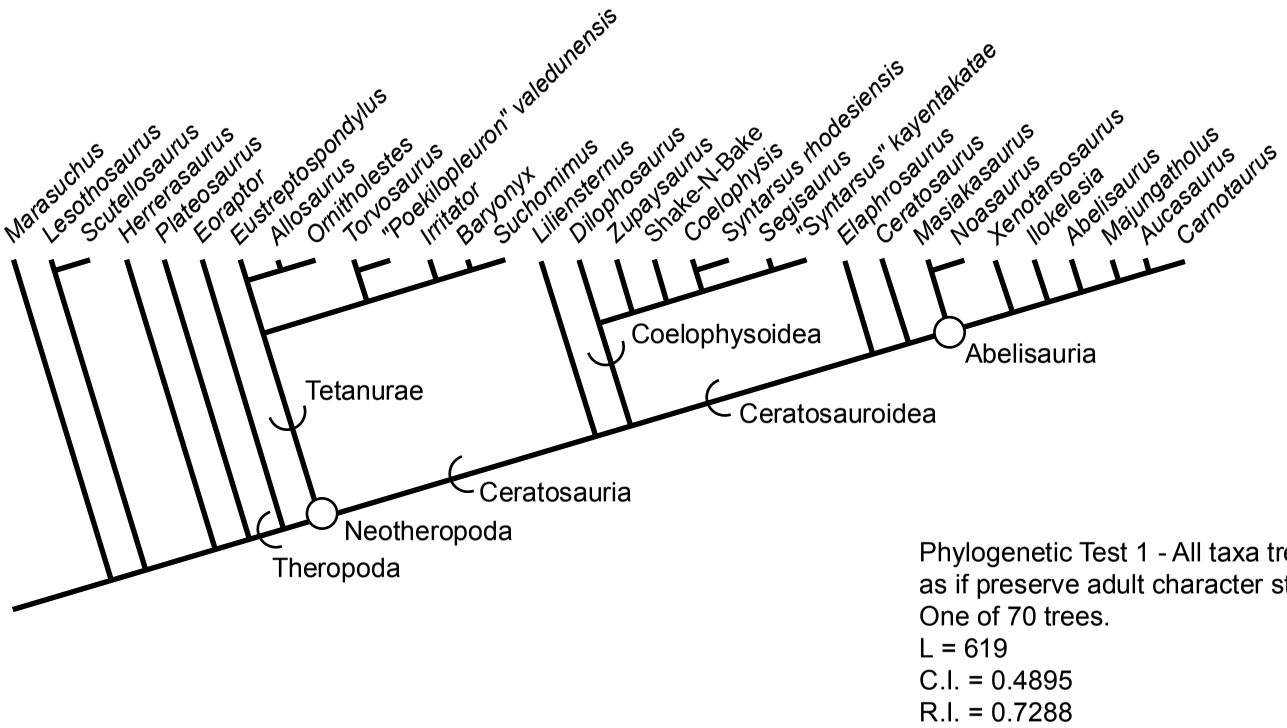


FIGURE 106C. Phylogenetic Test 1. One of 70 equally most parsimonious hypotheses of basal theropod phylogeny. All taxa were scored as if they were known from adult specimens. Length = 619, C.I.=0.4895, R.I.=0.7288. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

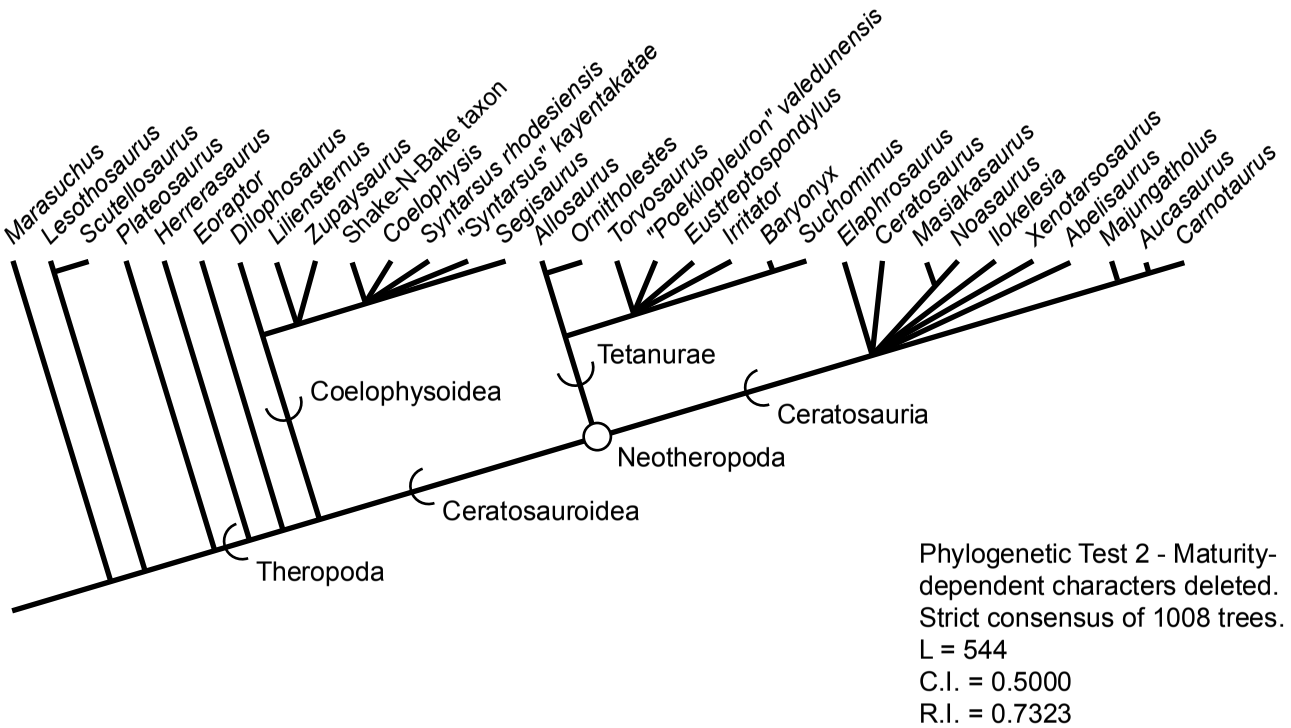


FIGURE 107A. Phylogenetic Test 2. Strict consensus tree of 1008 equally most parsimonious hypotheses of basal theropod phylogeny. Maturity-dependent characters were deleted from the analysis (see Table 6 for list of deleted characters). Length = 544, C.I.=0.5000, R.I.=0.7323. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

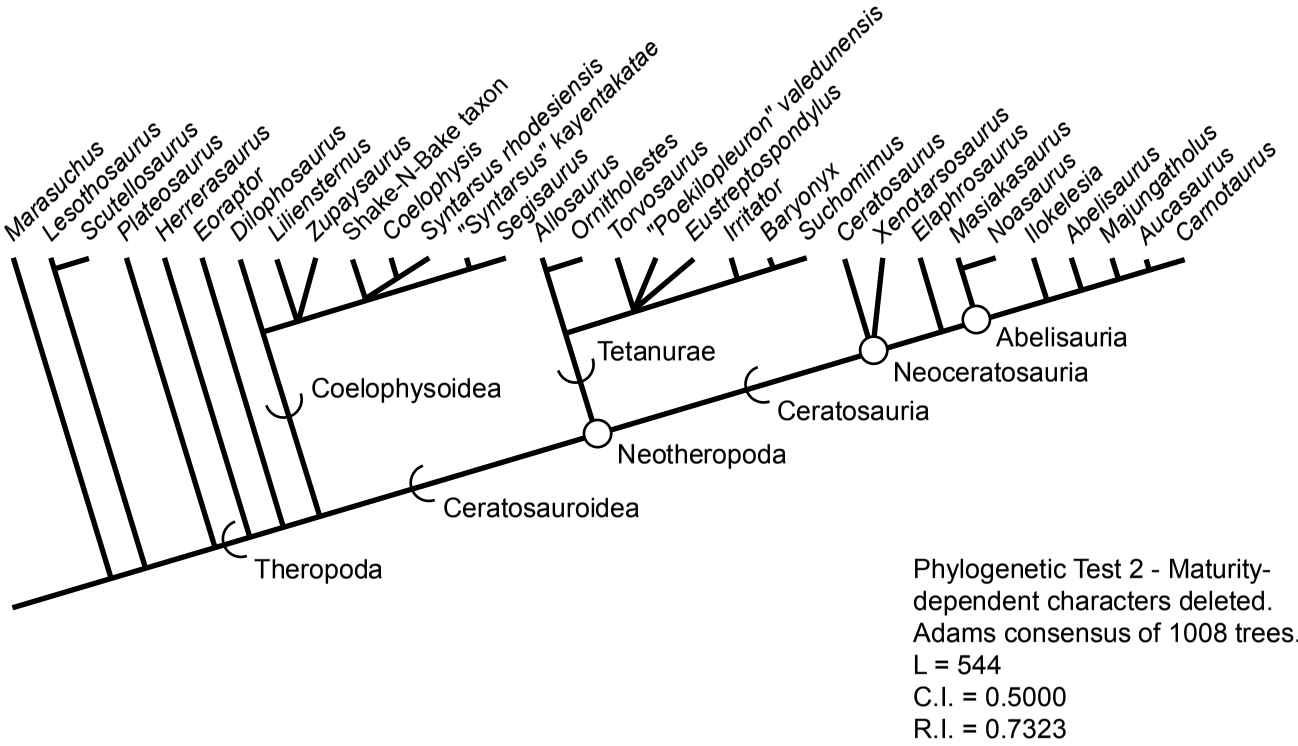


FIGURE 107B. Phylogenetic Test 2. Adams consensus tree of 1008 equally most parsimonious hypotheses of basal theropod phylogeny. Maturity-dependent characters were deleted from the analysis (see Table 6 for list of deleted characters). Length = 544, C.I.=0.5000, R.I.=0.7323. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

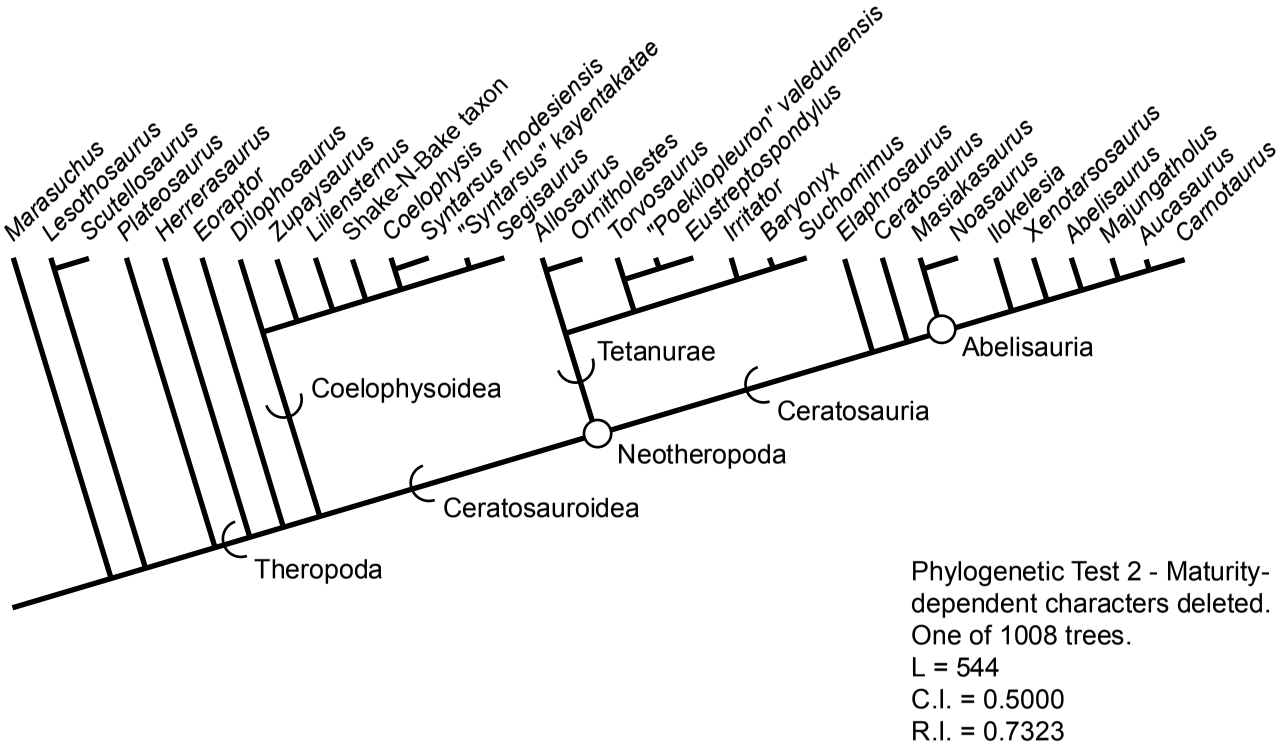


FIGURE 107C. Phylogenetic Test 2. One of 1008 equally most parsimonious hypotheses of basal theropod phylogeny. Maturity-dependent characters were deleted from the analysis (see Table 6 for list of deleted characters). Length = 544, C.I.=0.5000, R.I.=0.7323. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

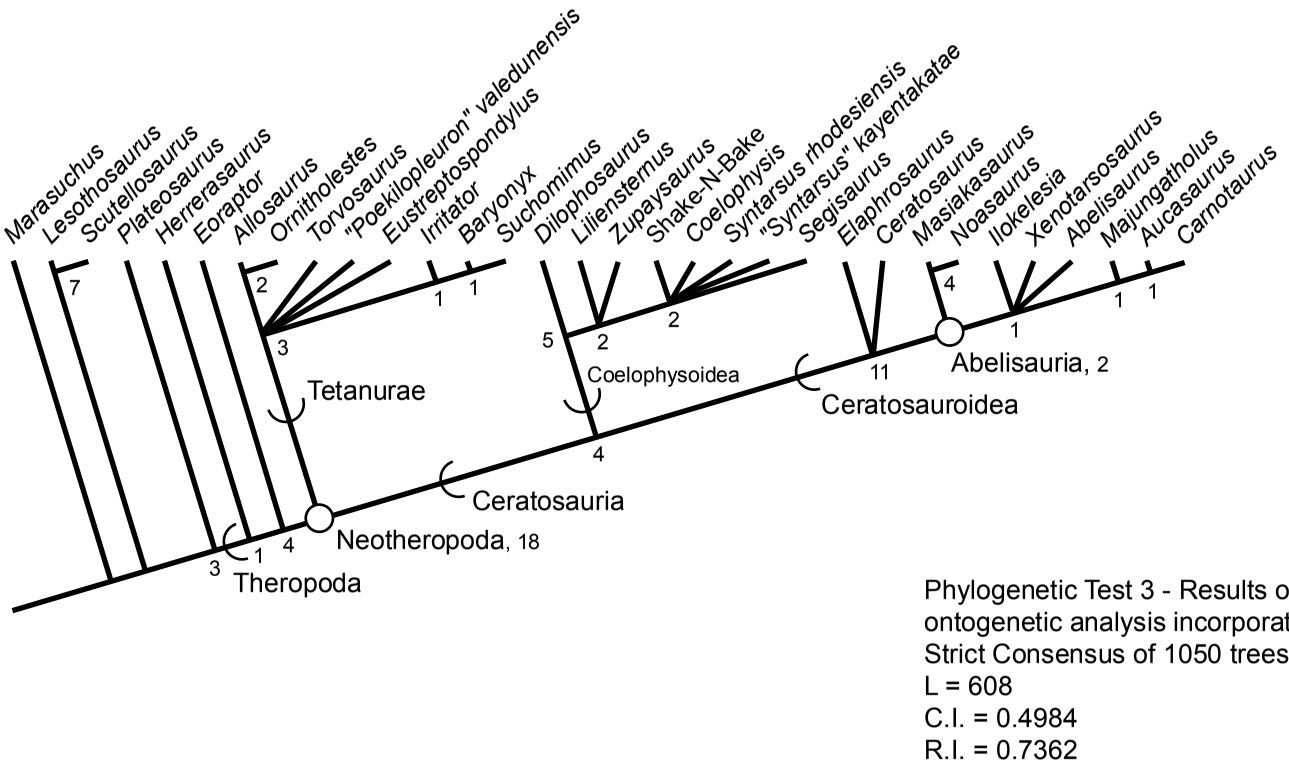


FIGURE 108A. Phylogenetic Test 3. Strict consensus tree of 1050 equally most parsimonious hypotheses of basal theropod phylogeny. Results of the ontogenetic analysis (Chapter 1) were used to code maturity-dependent characters for some taxa. Length = 608, C.I.=0.4984, R.I.=0.7362. Open circles denote node-defined clade names. Arcs denote stem-defined clade names. Numbers represent decay indices for nodes.

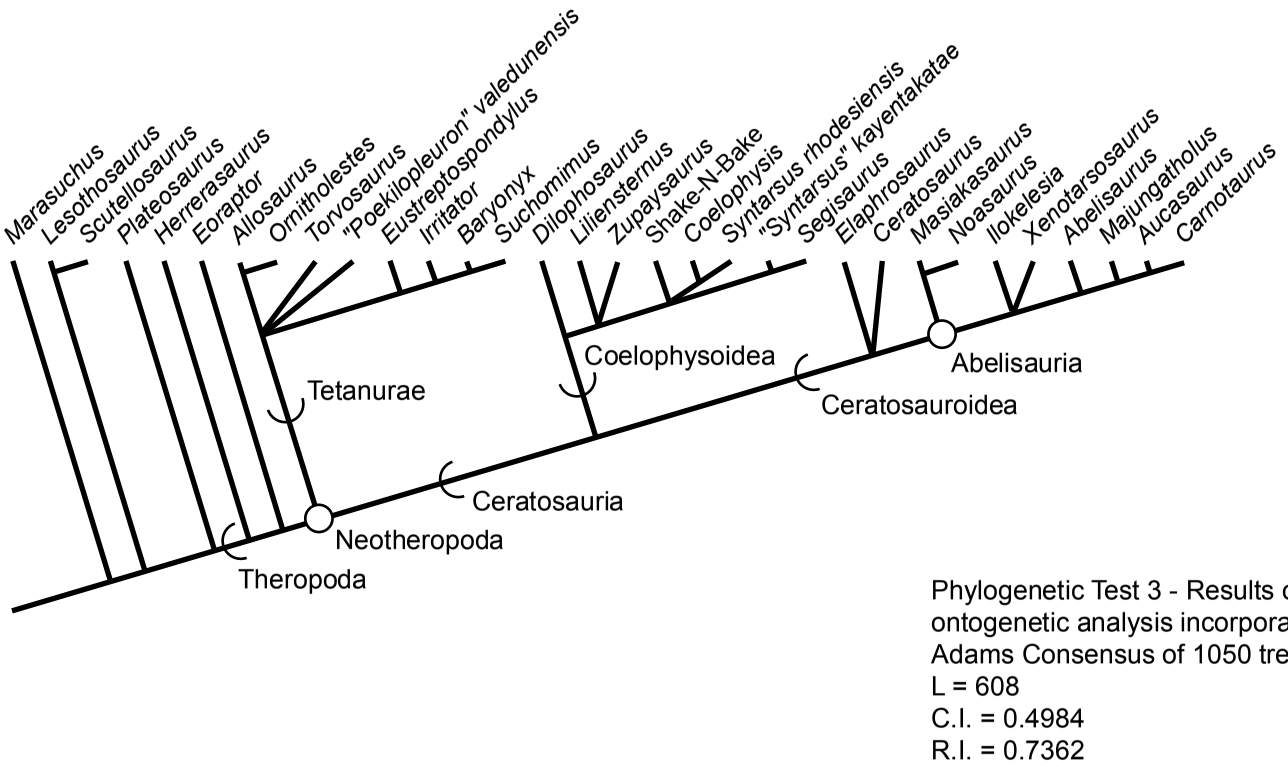
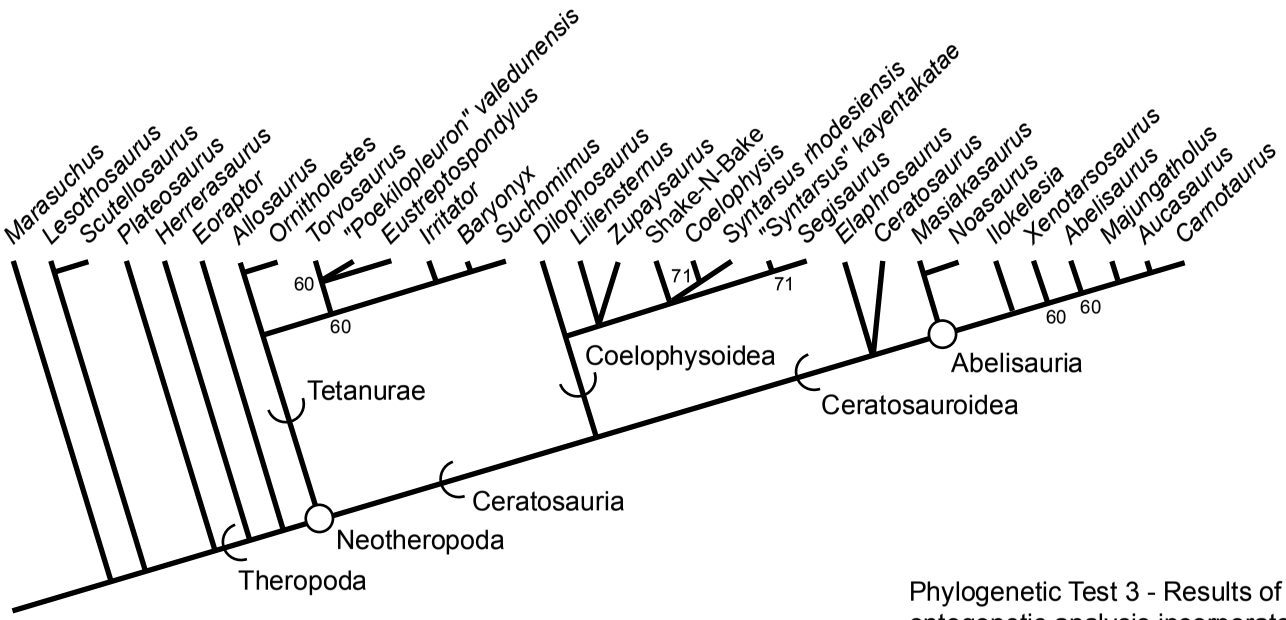


FIGURE 108B. Phylogenetic Test 3. Adams consensus tree of 1050 equally most parsimonious hypotheses of basal theropod phylogeny. Results of the ontogenetic analysis (Chapter 1) were used to code maturity-dependent characters for some taxa. Length = 608, C.I.=0.4984, R.I.=0.7362. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.



Phylogenetic Test 3 - Results of
ontogenetic analysis incorporated.
50% majority rule consensus of 1050 trees.
L = 608
C.I. = 0.4984
R.I. = 0.7362

FIGURE 108C. Phylogenetic Test 3. 50% majority rule consensus tree of 1050 equally most parsimonious hypotheses of basal theropod phylogeny. Results of the ontogenetic analysis (Chapter 1) were used to code maturity-dependent characters for some taxa. Length = 608, C.I.=0.4984, R.I.=0.7362. Nodes were recovered in 100% of trees unless otherwise noted above by percentage value next to node. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

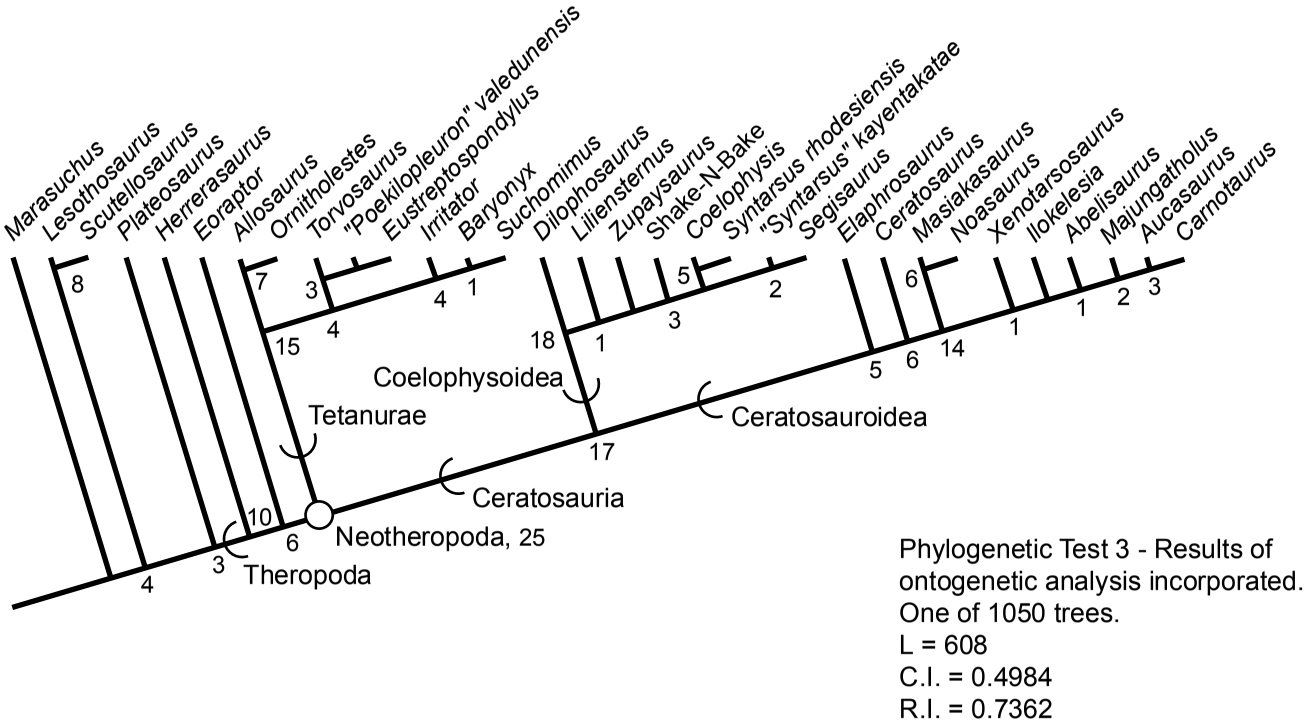


FIGURE 108D. Phylogenetic Test 3. One of 1050 equally most parsimonious hypotheses of basal theropod phylogeny. Results of the ontogenetic analysis (Chapter 1) were used to code maturity-dependent characters for some taxa. Length = 608, C.I.=0.4984, R.I.=0.7362. Open circles denote node-defined clade names. Arcs denote stem-defined clade names. Numbers represent number of unambiguous characters supporting each node.

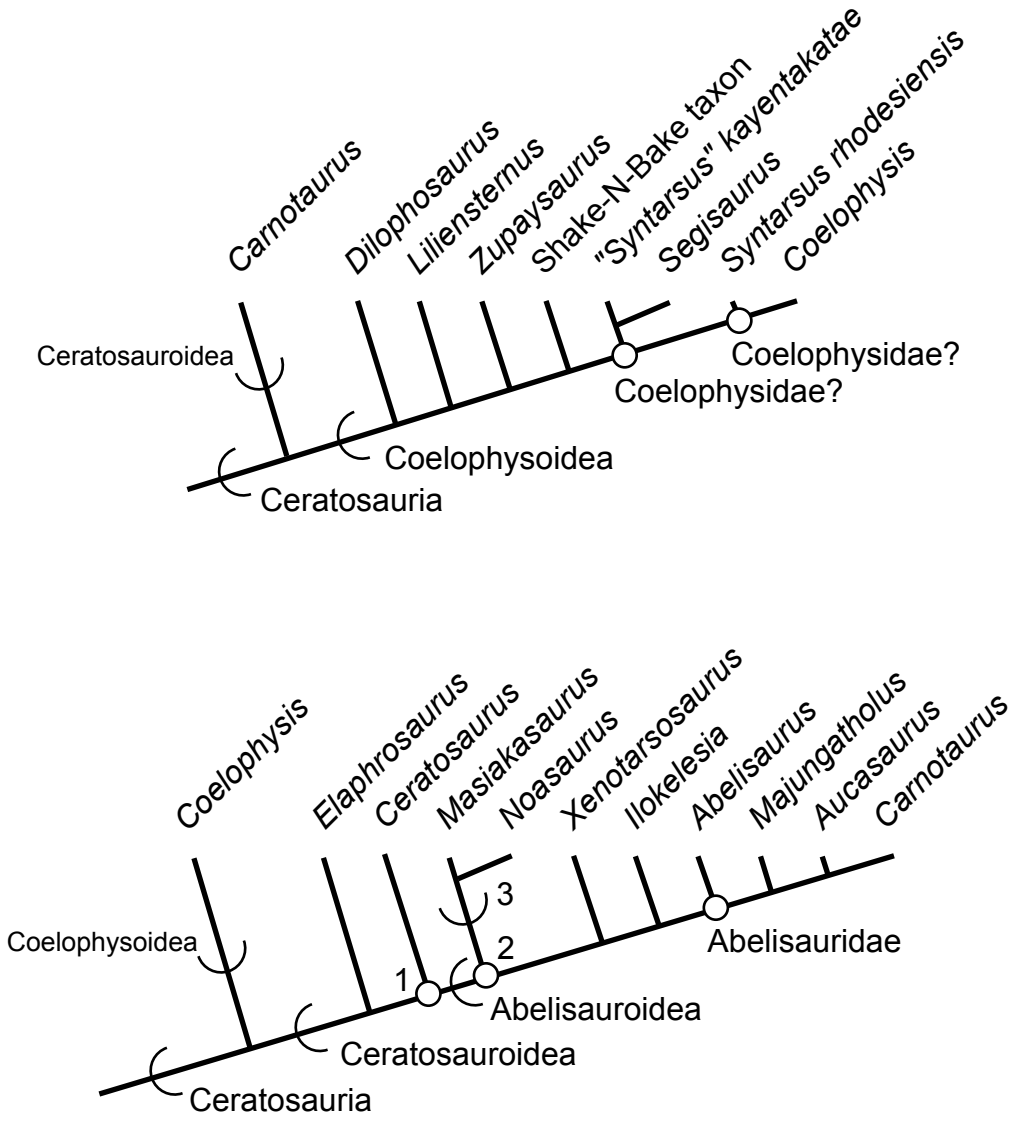


FIGURE 108E. Taxonomy within Ceratosauria. Clade topologies taken from tree illustrated in Figure 108D (one of 1050 equally parsimonious trees). Open circles indicate node-defined clade names. Arcs indicate stem-defined clade names. Numbered names in the ceratosauroid clade are, 1) Neoceratosauria, 2) Abelisauria, 3) Noasauridae. See Table 1 for phylogenetic definitions of clade names.

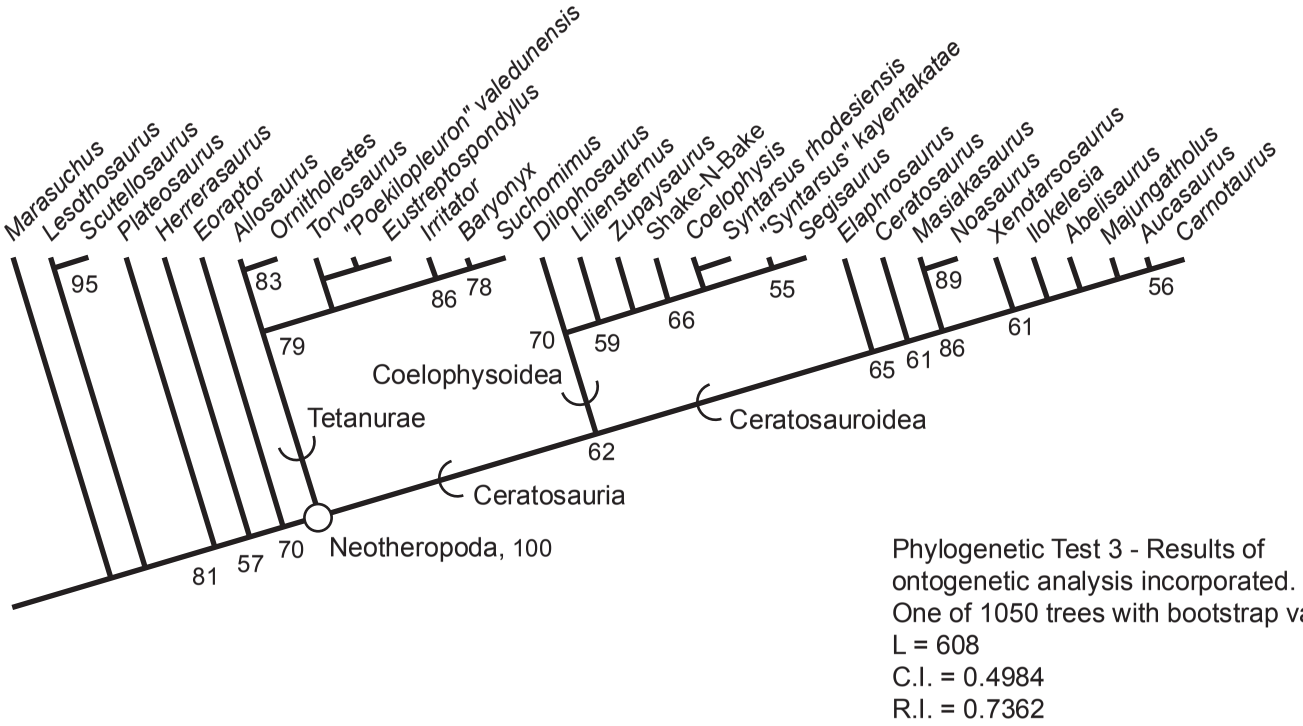


FIGURE 108F. Phylogenetic Test 3. One of 1050 equally most parsimonious hypotheses of basal theropod phylogeny with bootstrap values indicated. Results of the ontogenetic analysis (Chapter 1) were incorporated into character coding. Length = 608, C.I.=0.4984, R.I.=0.7362. Open circles denote node-defined clade names. Arcs denote stem-defined clade names. Numbers indicate bootstrap values (1000 replicates) at nodes with at least 50% bootstrap support. Bootstrap numbers are rounded off in figure.

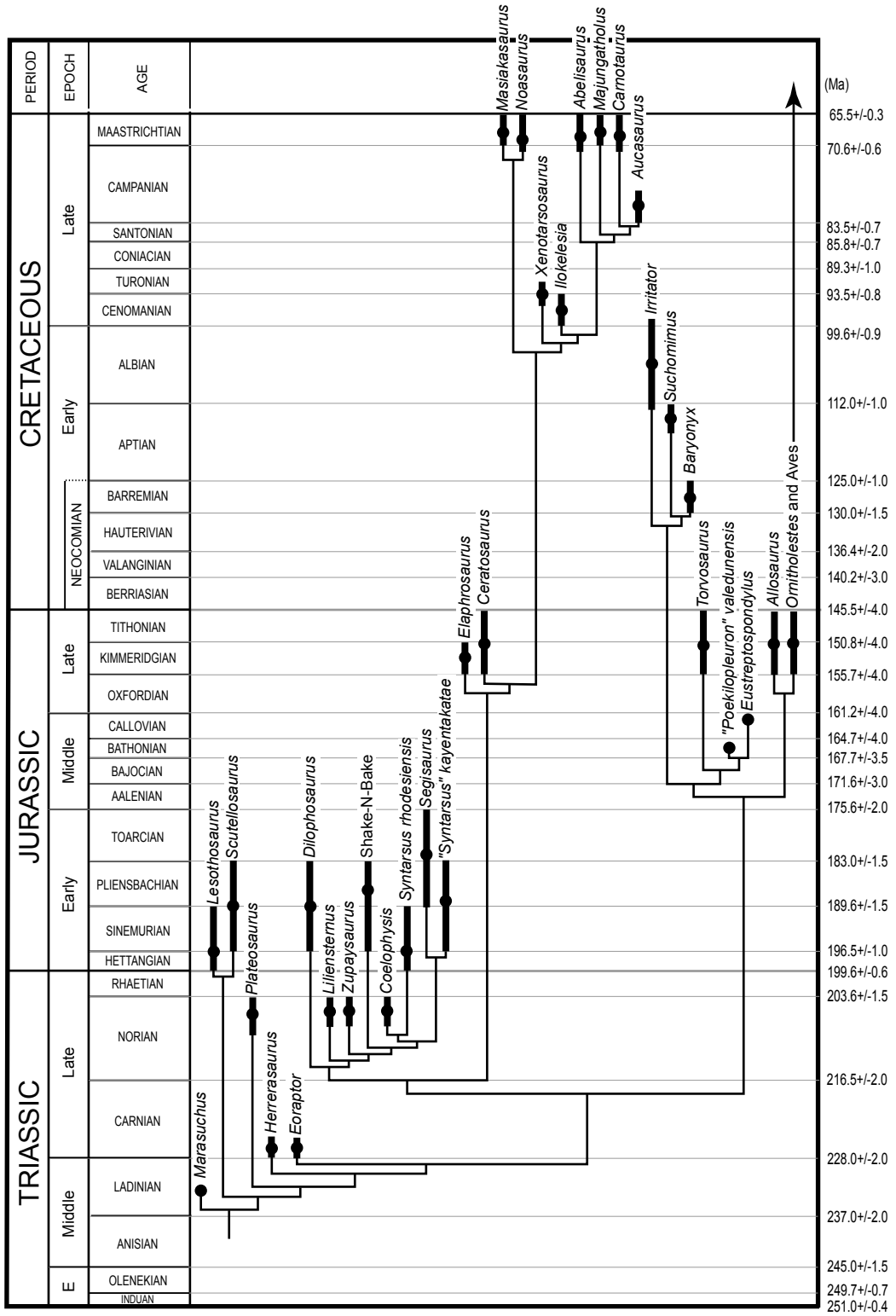


FIGURE 109. Phylogeny superimposed on geologic time scale. See text for explanation of conventions used in Figures 109, 111, 112D, 113D, 114D, 115D, 116D, and 118D.

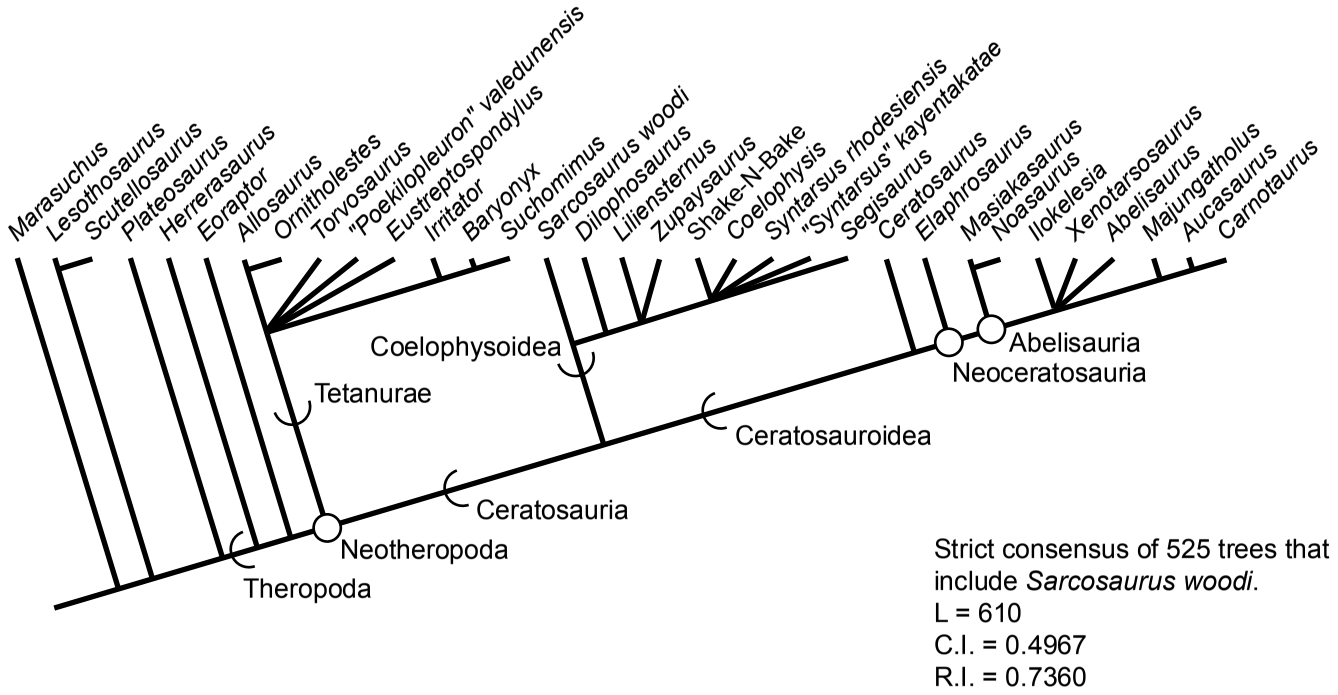


FIGURE 110. Strict consensus tree of 525 equally most parsimonious hypotheses of basal theropod phylogeny that include *Sarcosaurus woodi*. Length = 610, C.I.=0.4967, R.I.=0.7360. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

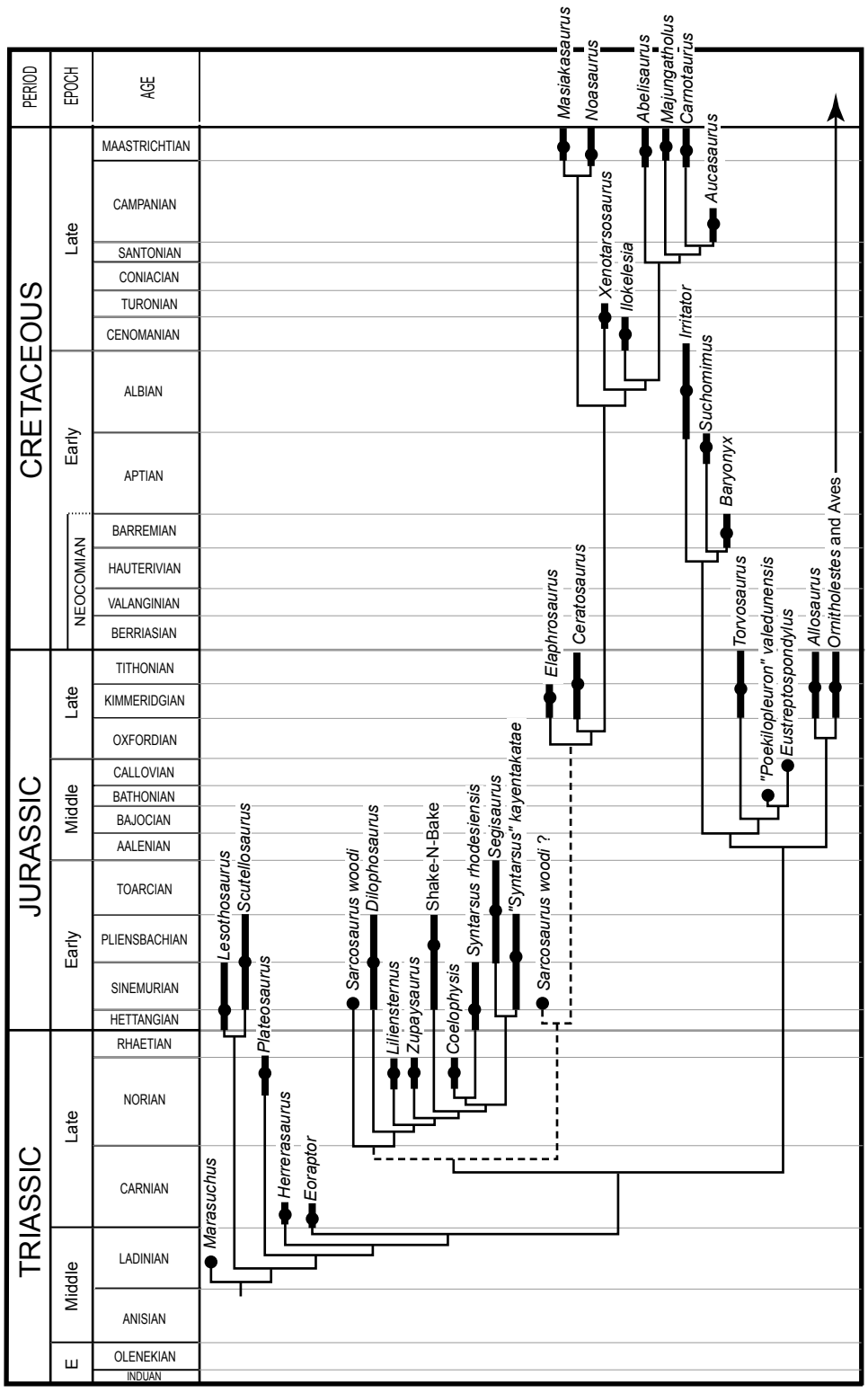


FIGURE 111. Phylogeny including *Sarcosaurus woodi* on the geologic time scale. Dashed branches indicate alternative relationships if *Sarcosaurus* were found to be a basal ceratosauroid . See text explanation of Figure 109 for further details of conventions used in this figure.

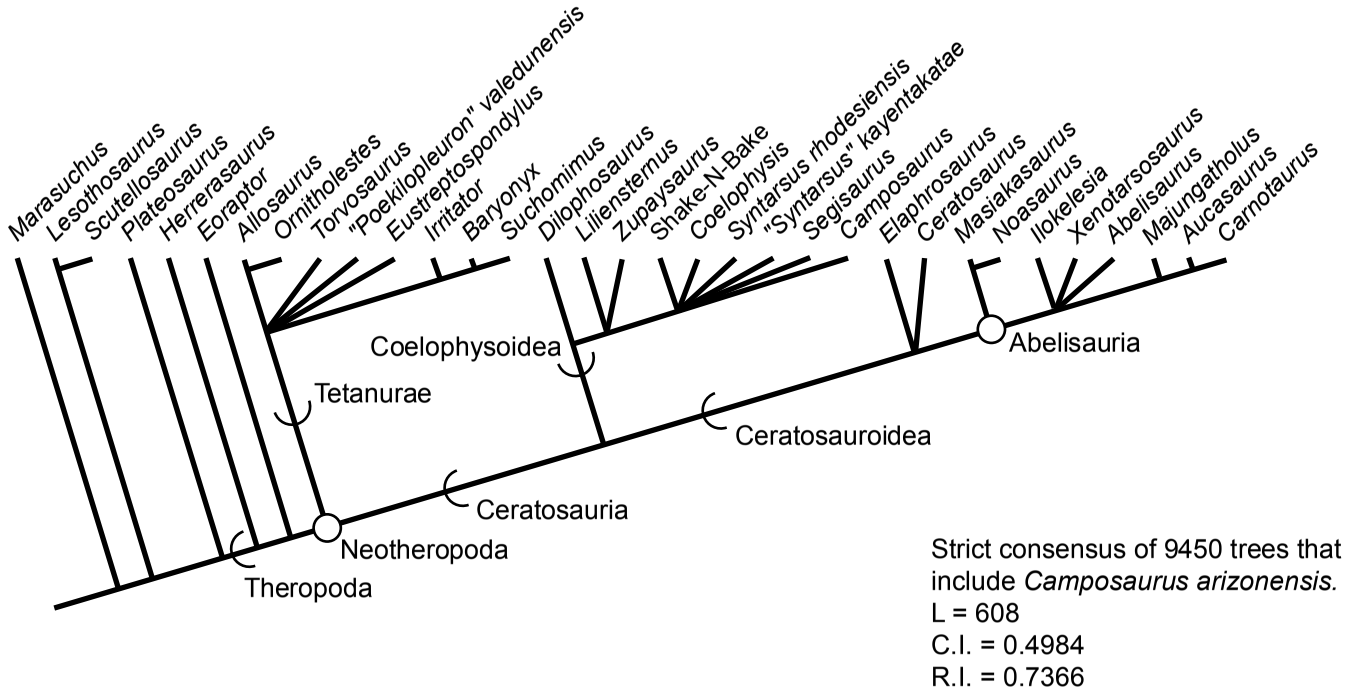


FIGURE 112A. Strict consensus tree of 9450 equally most parsimonious hypotheses of basal theropod phylogeny that include *Camposaurus arizonensis*. Length = 608, C.I.=0.4984, R.I.=0.7366. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

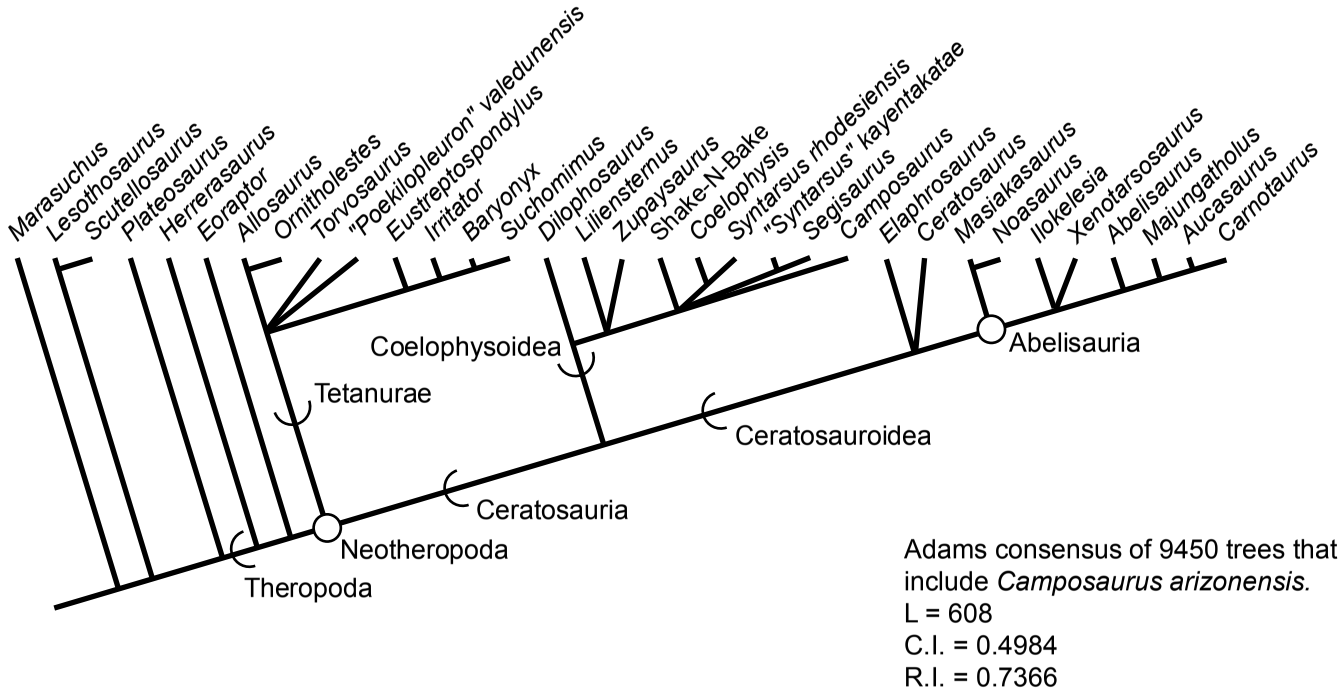


FIGURE 112B. Adams consensus tree of 9450 equally most parsimonious hypotheses of basal theropod phylogeny that include *Camposaurus arizonensis*. Length = 608, C.I.=0.4984, R.I.=0.7366. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

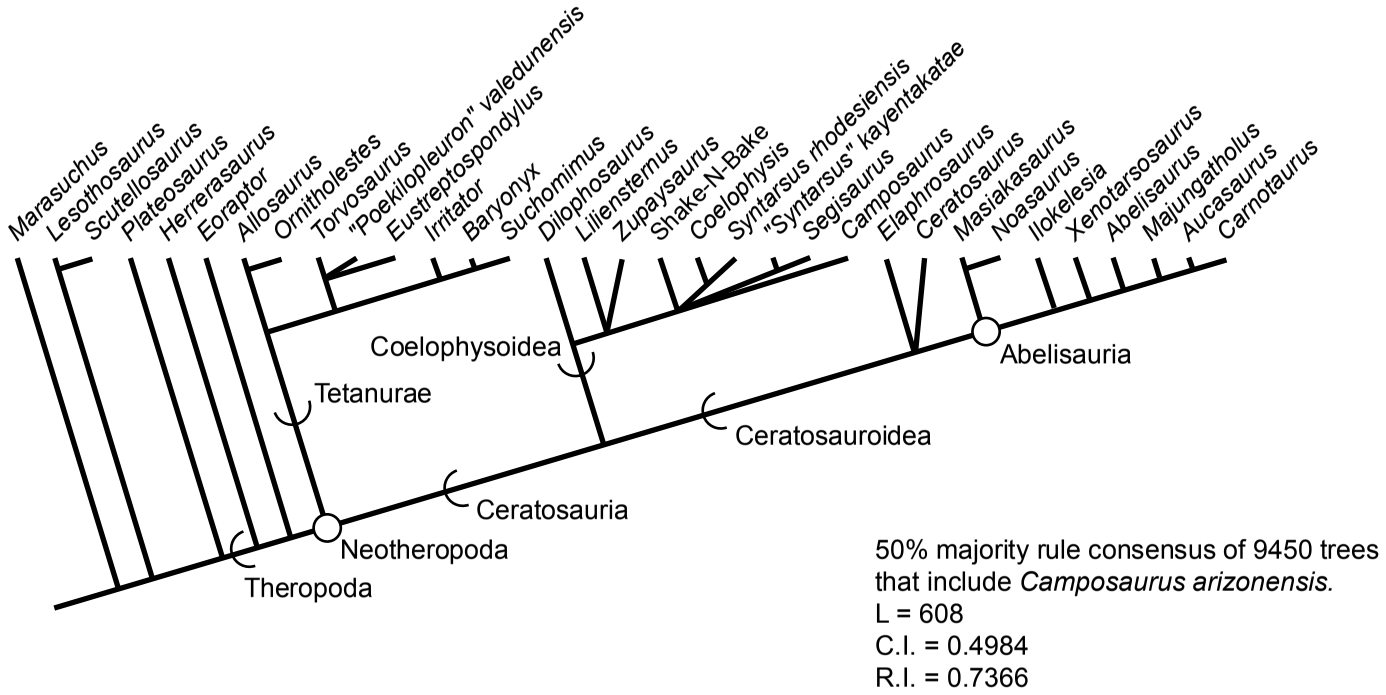


FIGURE 112C. 50% majority rule consensus tree of 9450 equally most parsimonious hypotheses of basal theropod phylogeny that include *Camposaurus arizonensis*. Length = 608, C.I.=0.4984, R.I.=0.7366. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

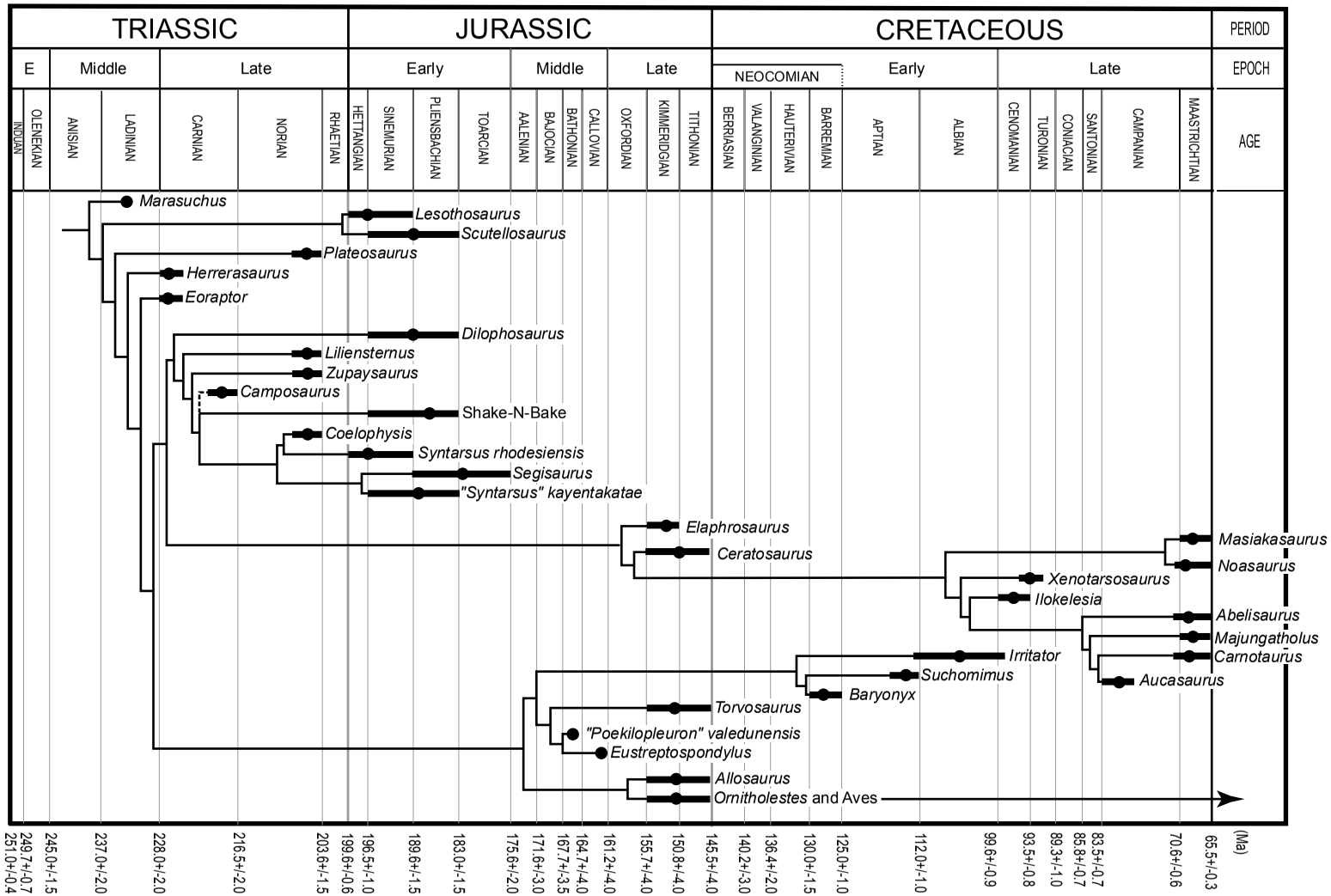


FIGURE 112D. Phylogeny based on cladogram in Figure 108D superimposed on the geologic time scale, but includes *Camposaurus arizonensis*. Dashed branches indicate possible relationships for *Camposaurus* relative to other ceratosaurs. See text explanation of Figure 109 for further details of conventions used in this figure.

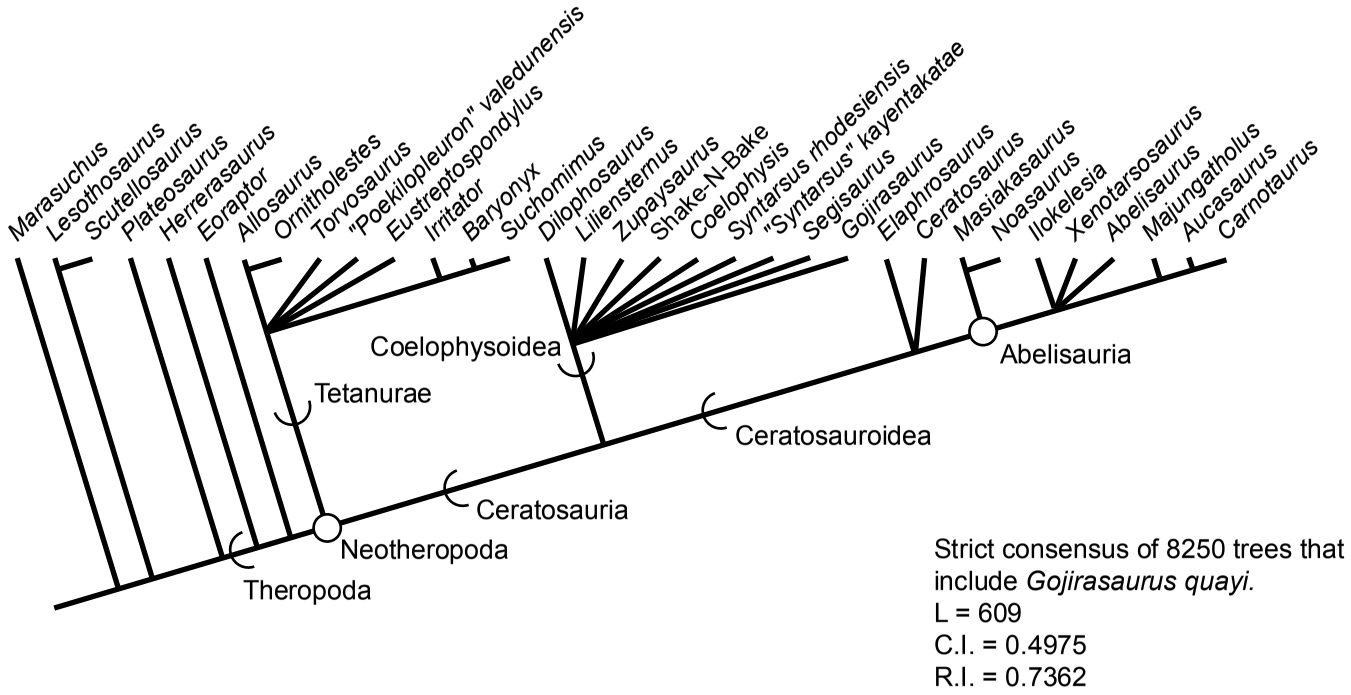


FIGURE 113A. Strict consensus tree of 8250 equally most parsimonious hypotheses of basal theropod phylogeny that include *Gojirasaurus quayi*. Length = 609, C.I.=0.4975, R.I.=0.7362. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

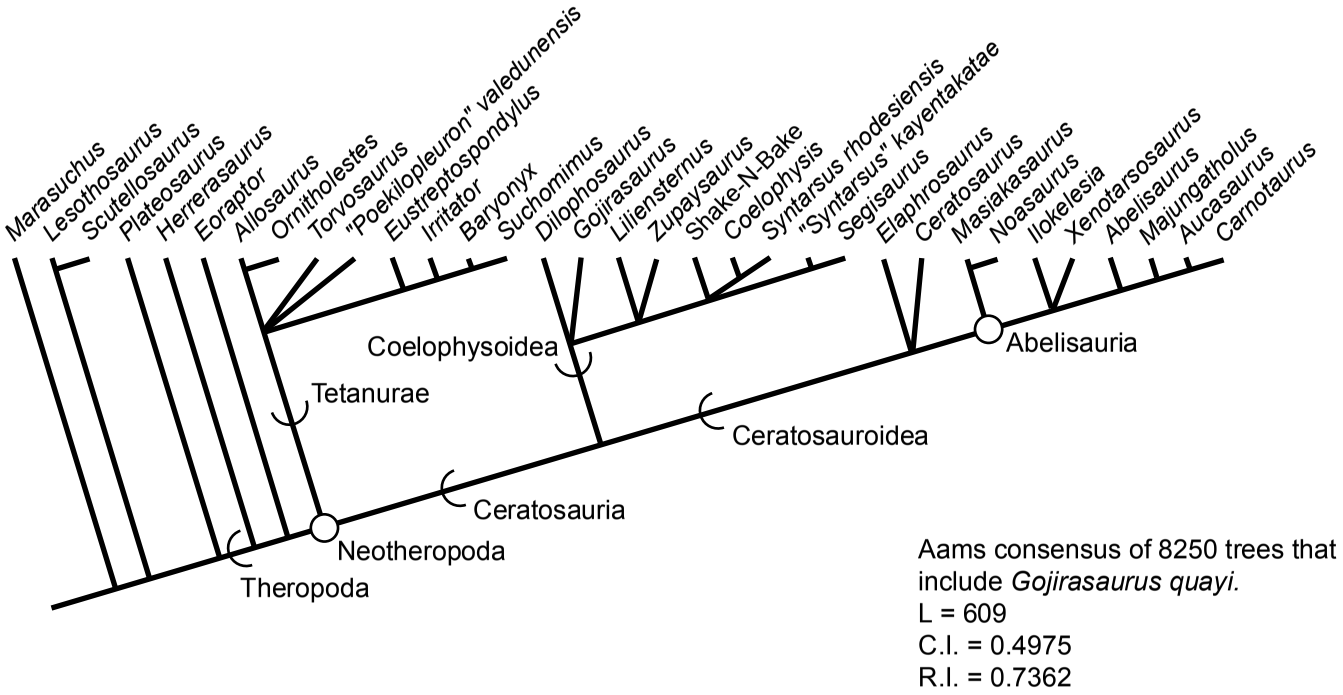


FIGURE 113B. Adams consensus tree of 8250 equally most parsimonious hypotheses of basal theropod phylogeny that include *Gojirasaurus quayi*. Length = 609, C.I.=0.4975, R.I.=0.7362. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

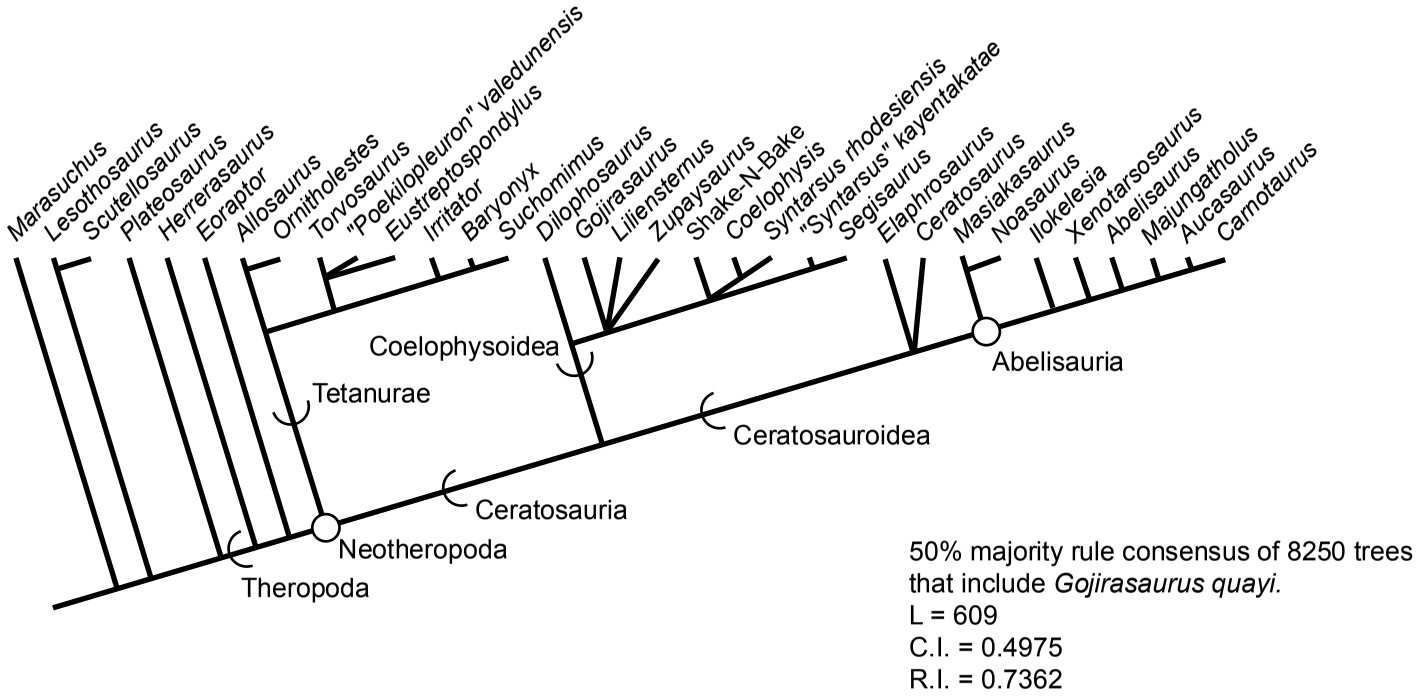


FIGURE 113C. 50% majority rule consensus tree of 8250 equally most parsimonious hypotheses of basal theropod phylogeny that include *Gojirasaurus quayi*. Length = 609, C.I.=0.4975, R.I.=0.7362. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

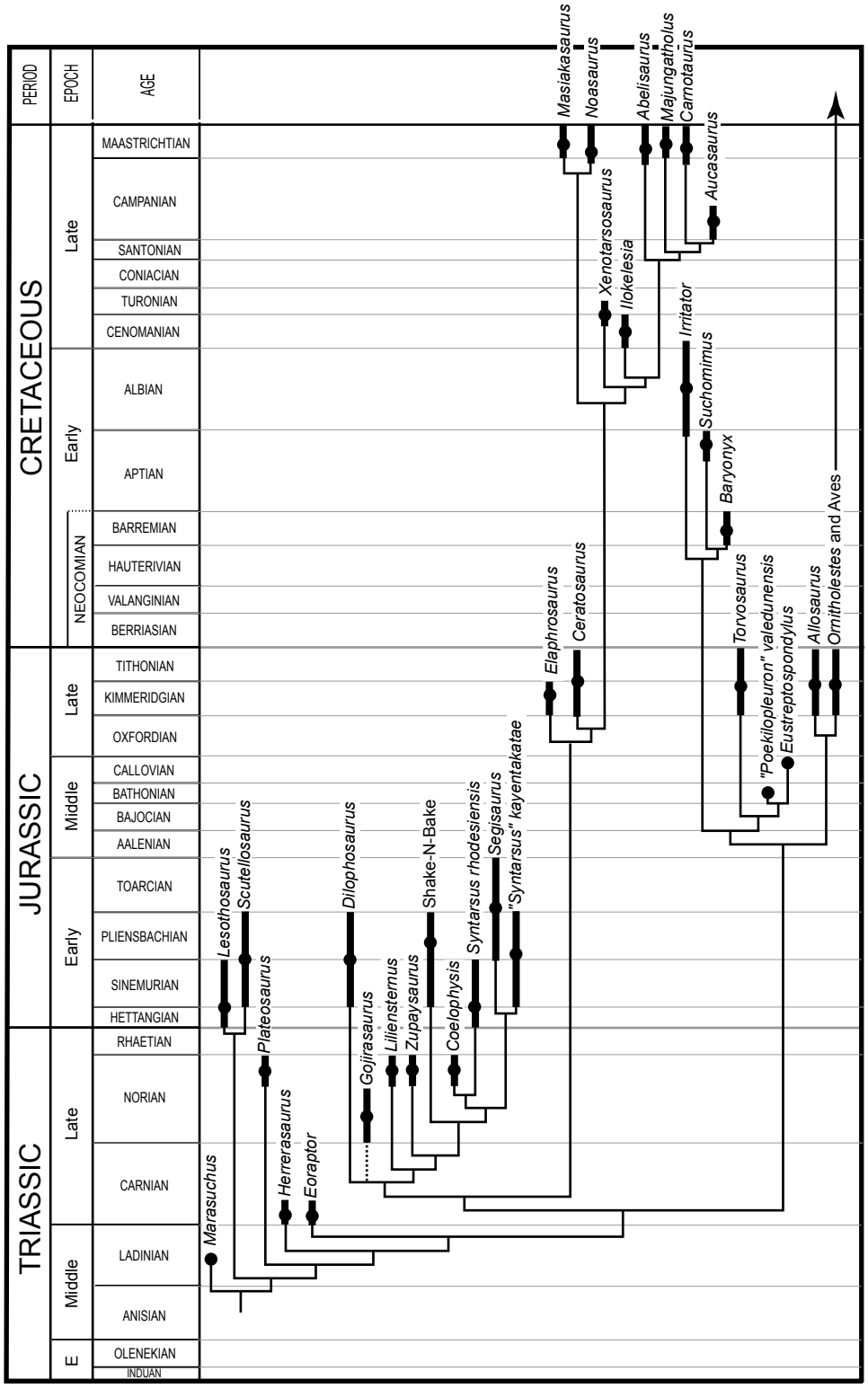


FIGURE 113D. Phylogeny based on cladogram in Figure 108D superimposed on the geologic time scale, but includes *Gojirasaurus quayi*. Dashed branches indicate possible relationships for *Gojirasaurus* relative to other ceratosaurs. See text explanation of Figure 109 for further details of conventions used in this figure.

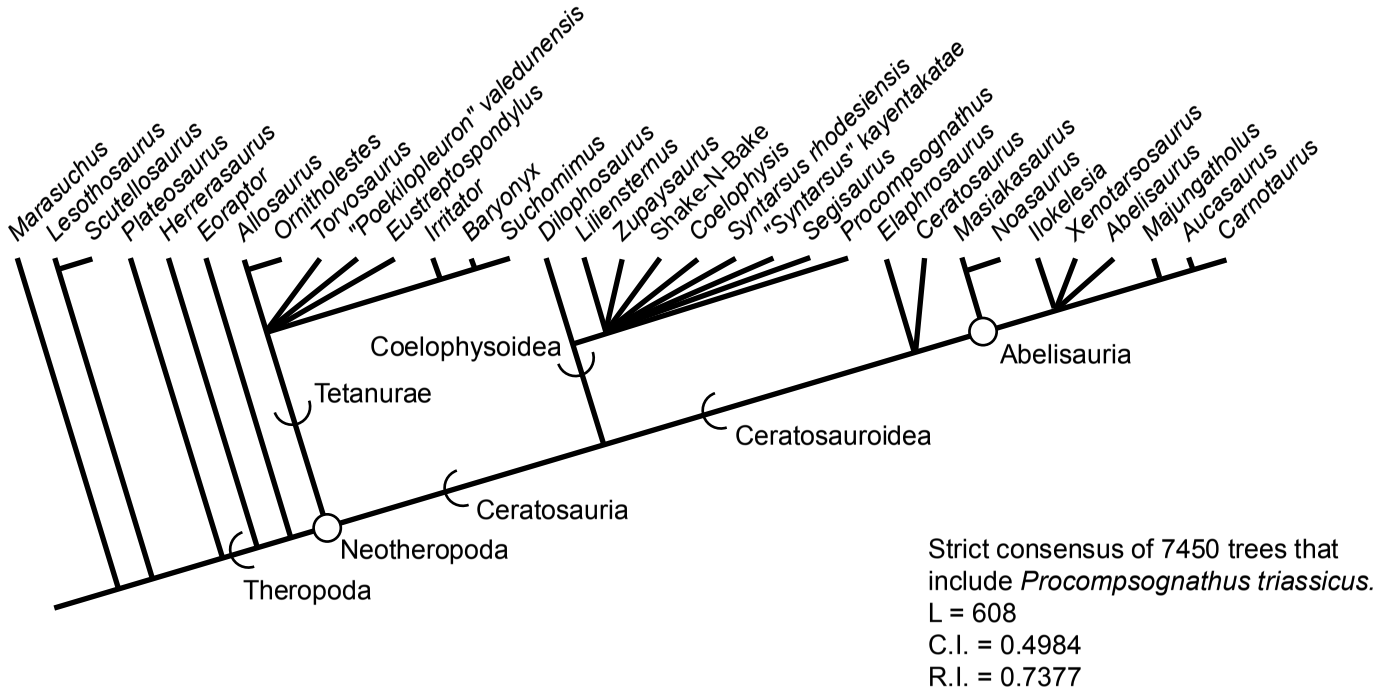


FIGURE 114A. Strict consensus tree of 7450 equally most parsimonious hypotheses of basal theropod phylogeny that include *Procompsognathus triassicus*. Length = 608, C.I.=0.4984, R.I.=0.7377. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

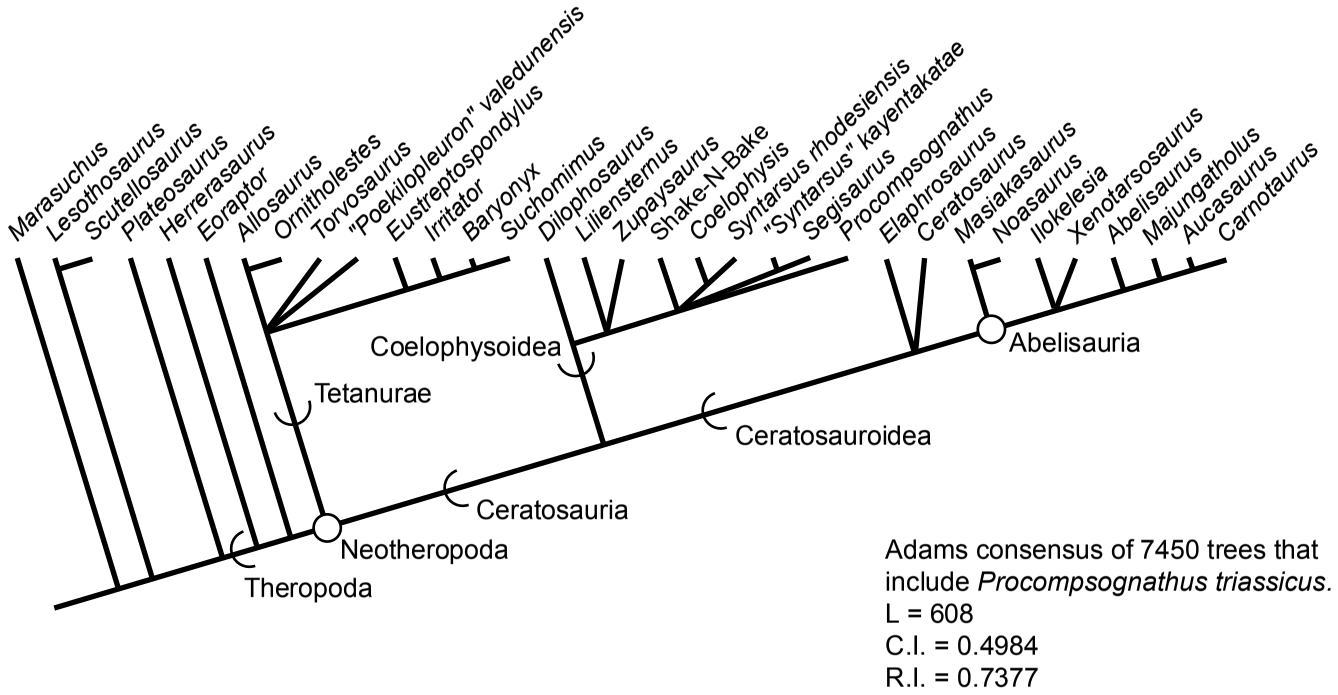


FIGURE 114B. Adams consensus tree of 7450 equally most parsimonious hypotheses of basal theropod phylogeny that include *Procompsognathus triassicus*. Length = 608, C.I.=0.4984, R.I.=0.7377. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

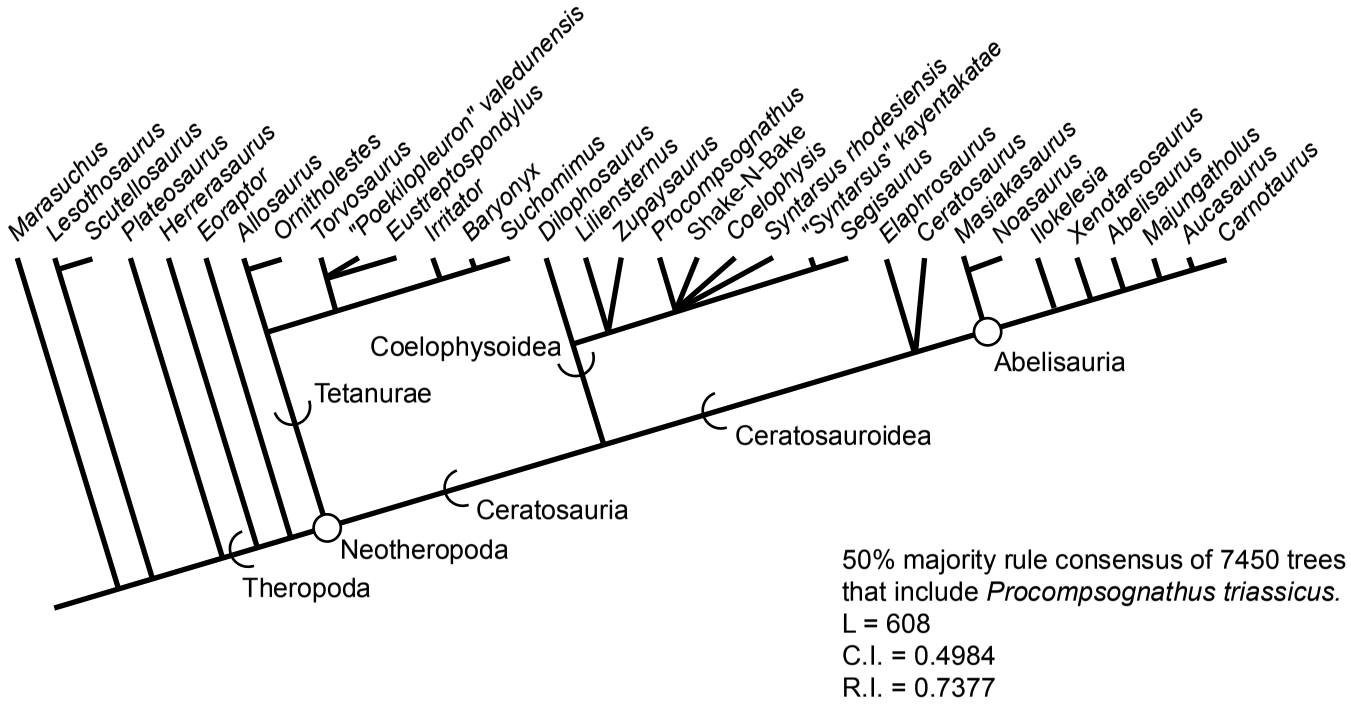


FIGURE 114C. 50% majority rule consensus tree of 7450 equally most parsimonious hypotheses of basal theropod phylogeny that include *Procompsognathus triassicus*. Length = 608, C.I.=0.4984, R.I.=0.7377. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

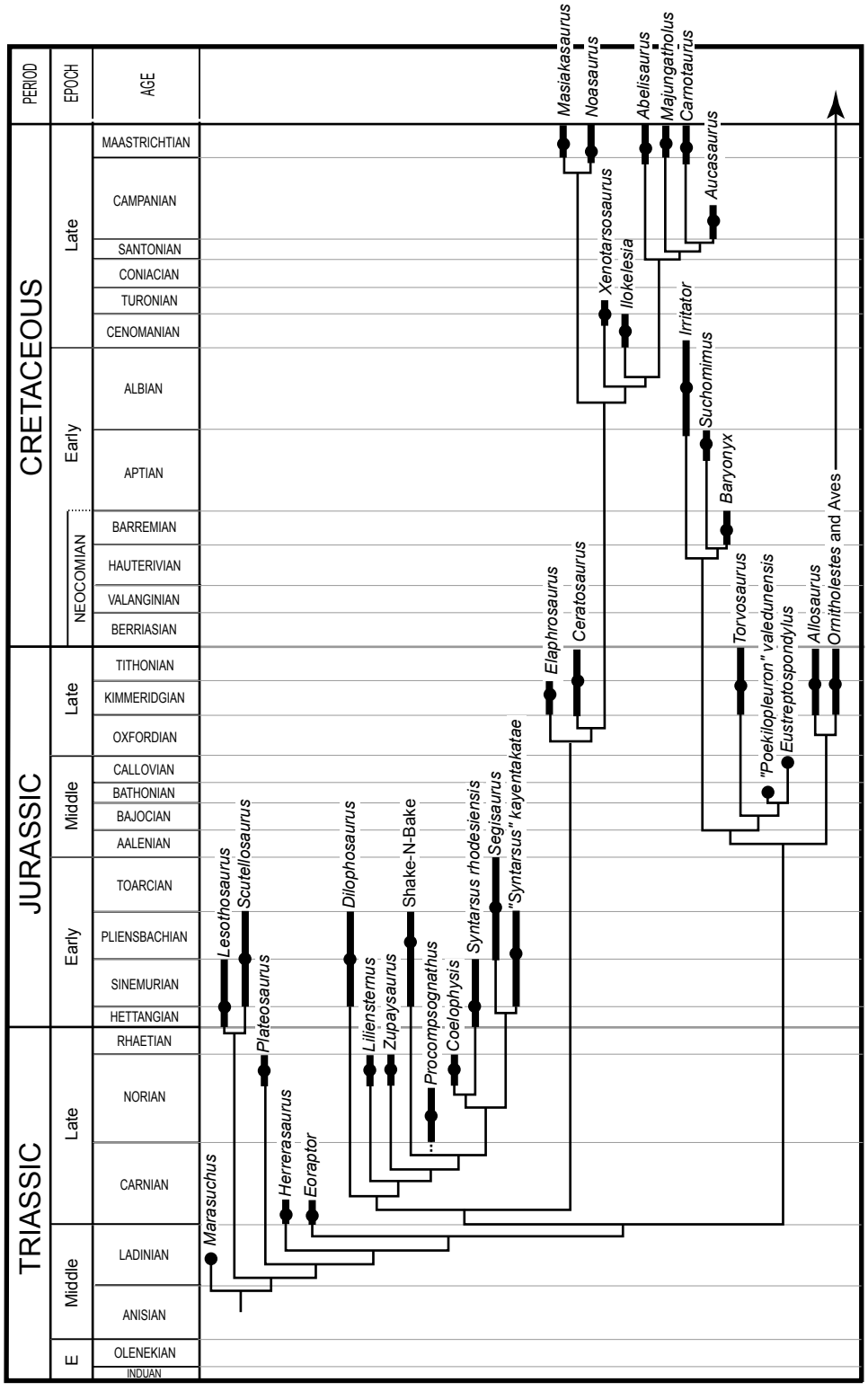


FIGURE 114D. Phylogeny based on cladogram in Figure 108D superimposed on the geologic time scale, but includes *Procompsognathus triassicus*. Dashed branches indicate possible relationships for *Procompsognathus* relative to other ceratosaurs. See text explanation of Figure 109 for further details of conventions used in this figure.

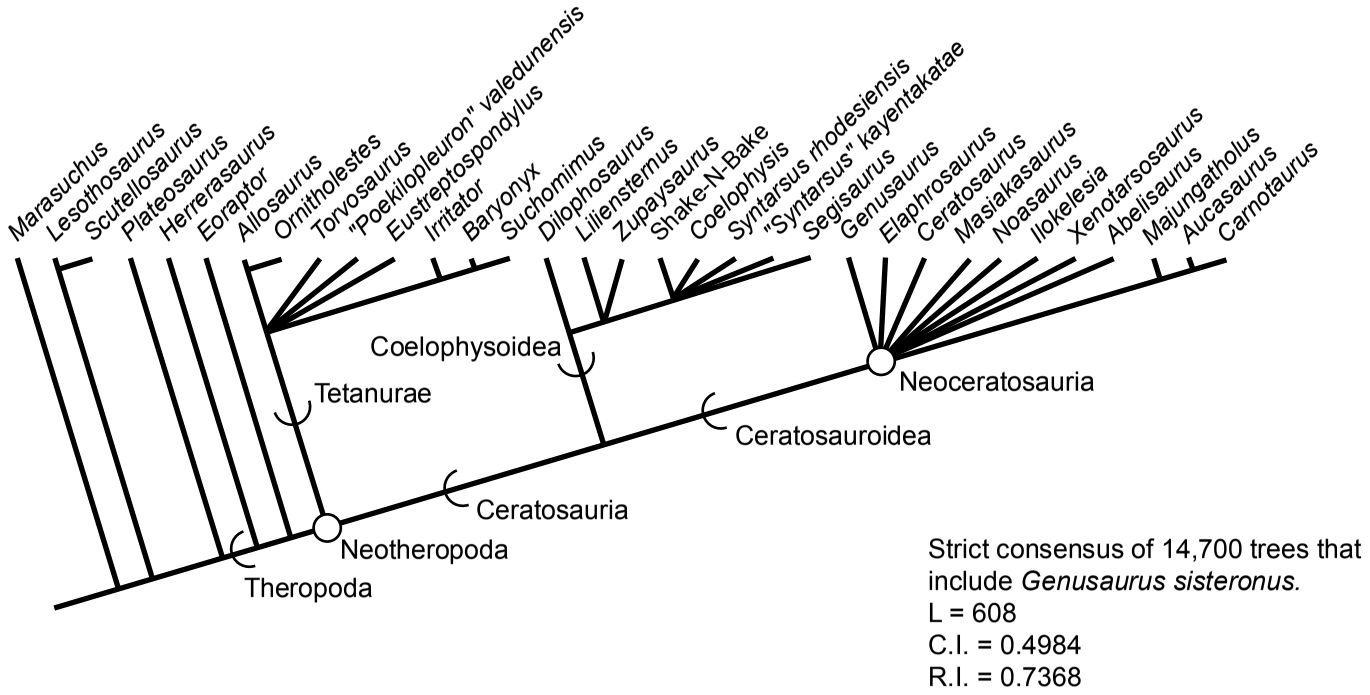


FIGURE 115A. Strict consensus tree of 14,700 equally most parsimonious hypotheses of basal theropod phylogeny that include *Genusaurus sisteronus*. Length = 630, C.I.=0.4984, R.I.=0.7368. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

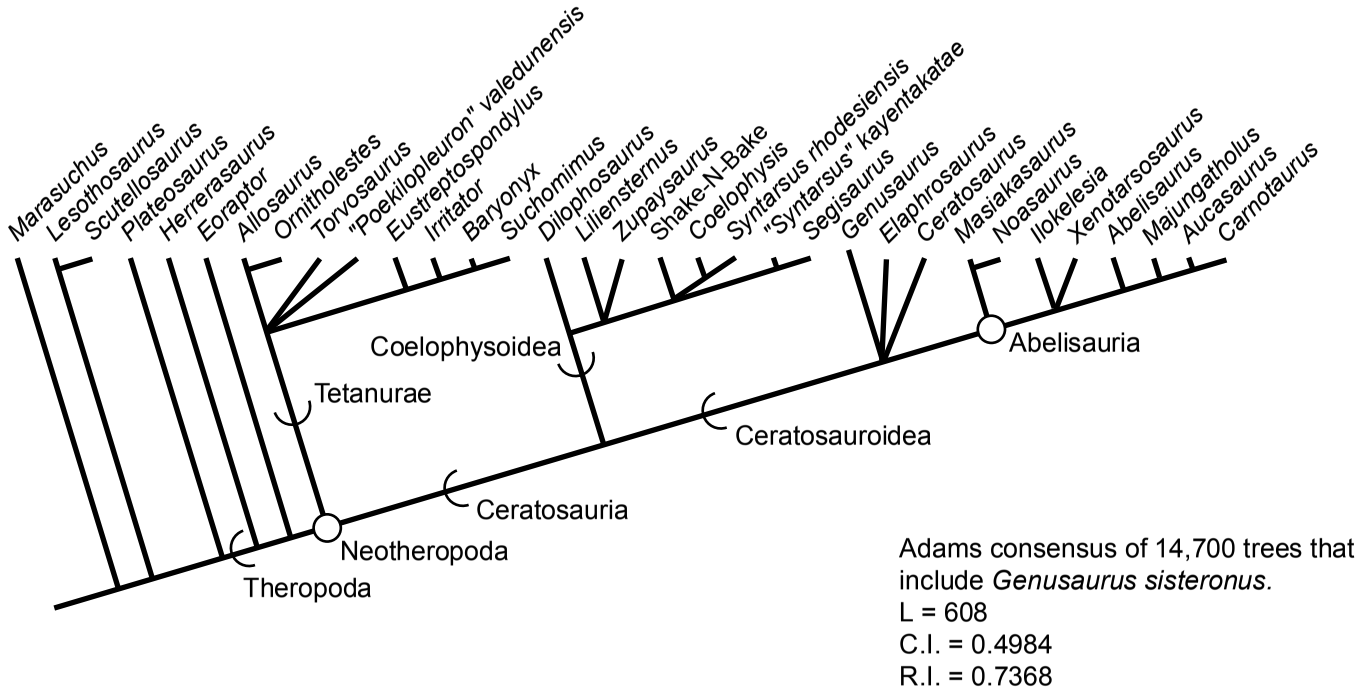


FIGURE 115B. Adams consensus tree of 14,700 equally most parsimonious hypotheses of basal theropod phylogeny that include *Genusaurus sisteronus*. Length = 630, C.I.=0.4984, R.I.=0.7368. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

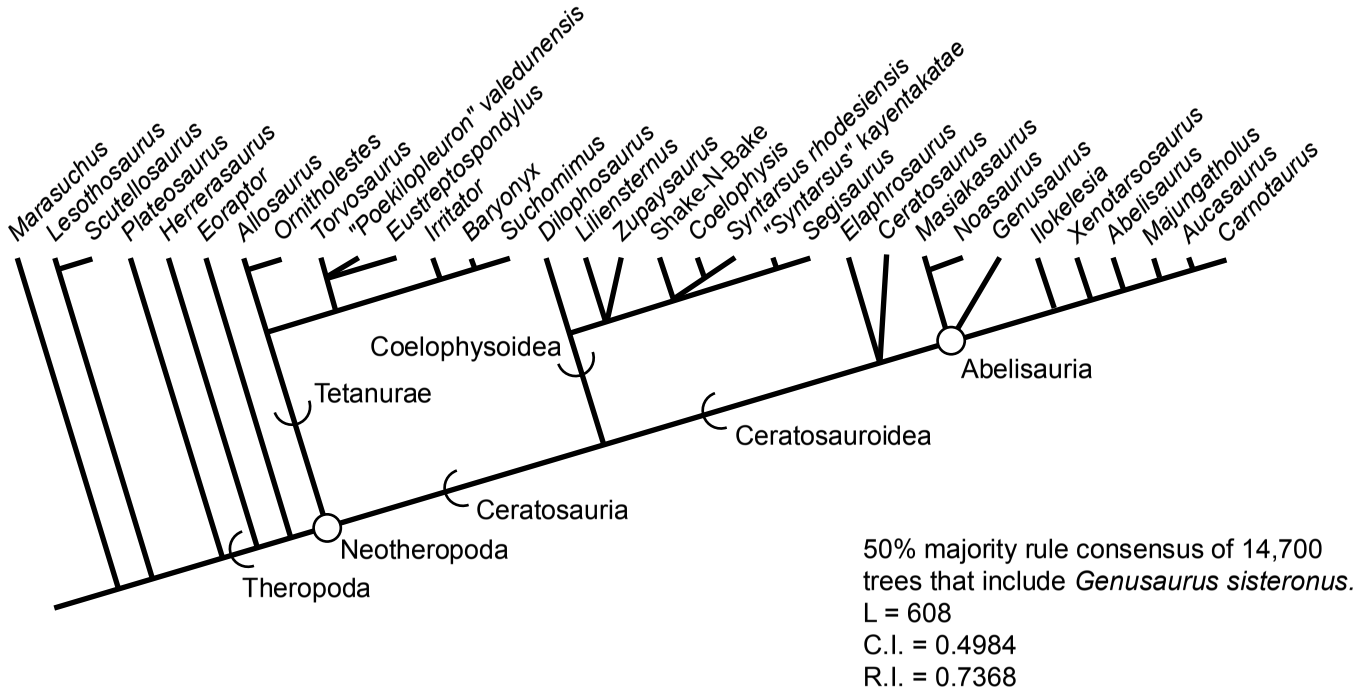


FIGURE 115C. 50% majority rule consensus tree of 14,700 equally most parsimonious hypotheses of basal theropod phylogeny that include *Genusaurus sisteronus*. Length = 630, C.I.=0.4984, R.I.=0.7368. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

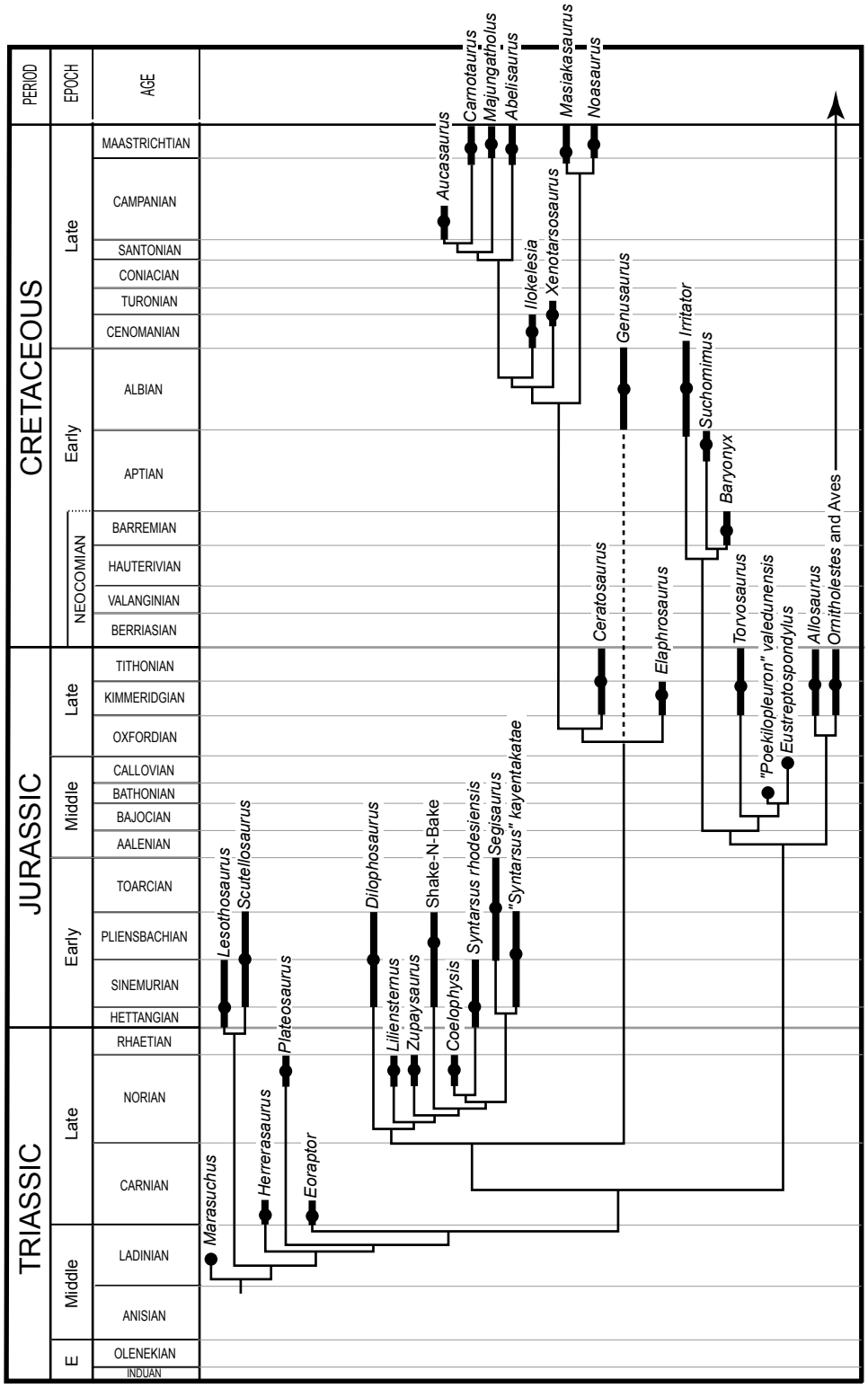


FIGURE 115D. Phylogeny including *Genusaurus sisteronus* on the geologic time scale. Dashed branches indicate possible relationships for *Genusaurus* relative to other ceratosaurs. See text explanation of Figure 109 for further details of conventions used in this figure.

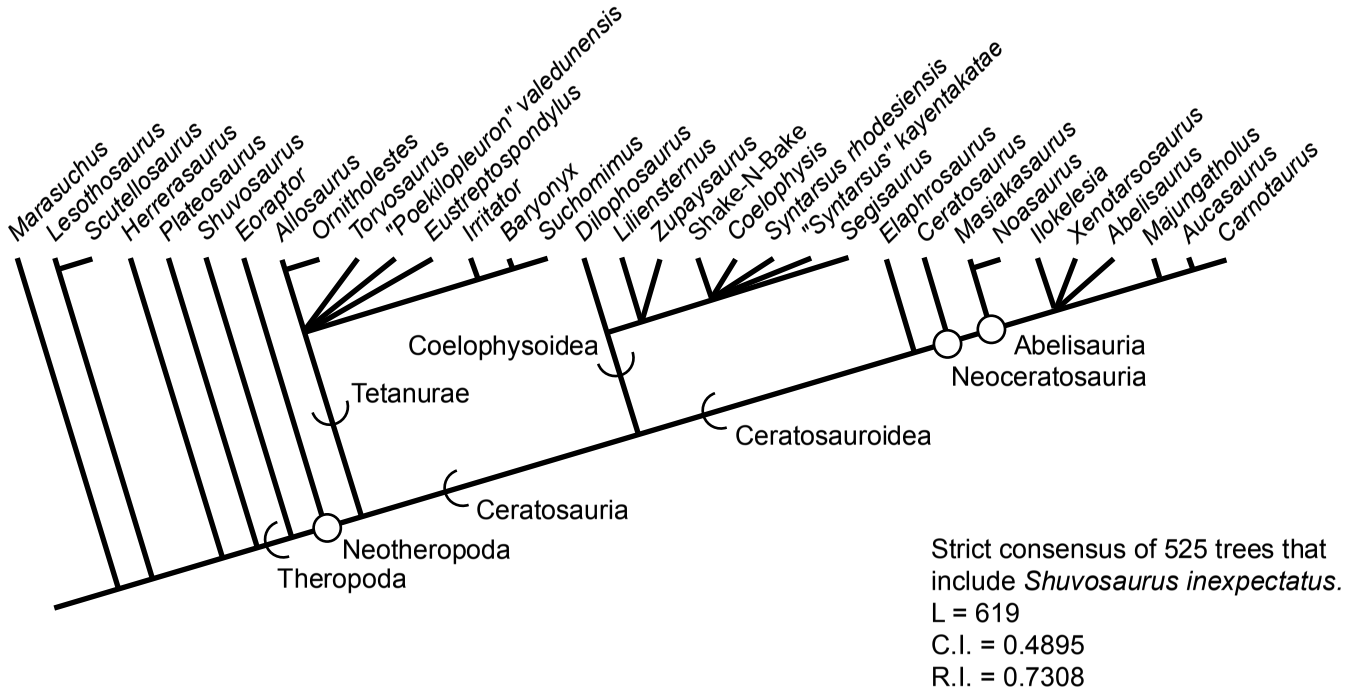


FIGURE 116A. Strict consensus tree of 525 equally most parsimonious hypotheses of basal theropod phylogeny that include *Shuvosaurus inexpectatus*. Length = 619, C.I.=0.4895, R.I.=0.7308. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

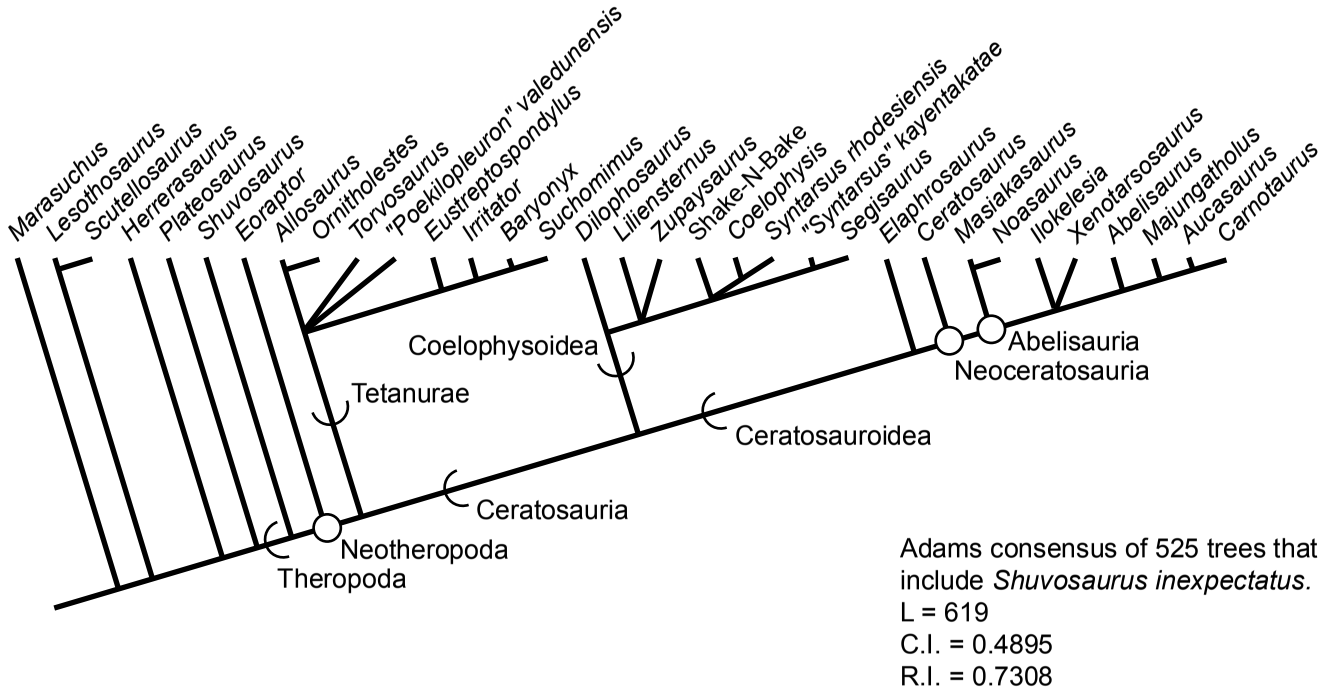


FIGURE 116B. Adams consensus tree of 525 equally most parsimonious hypotheses of basal theropod phylogeny that include *Shuvosaurus inexpectatus*. Length = 619, C.I.=0.4895, R.I.=0.7308. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

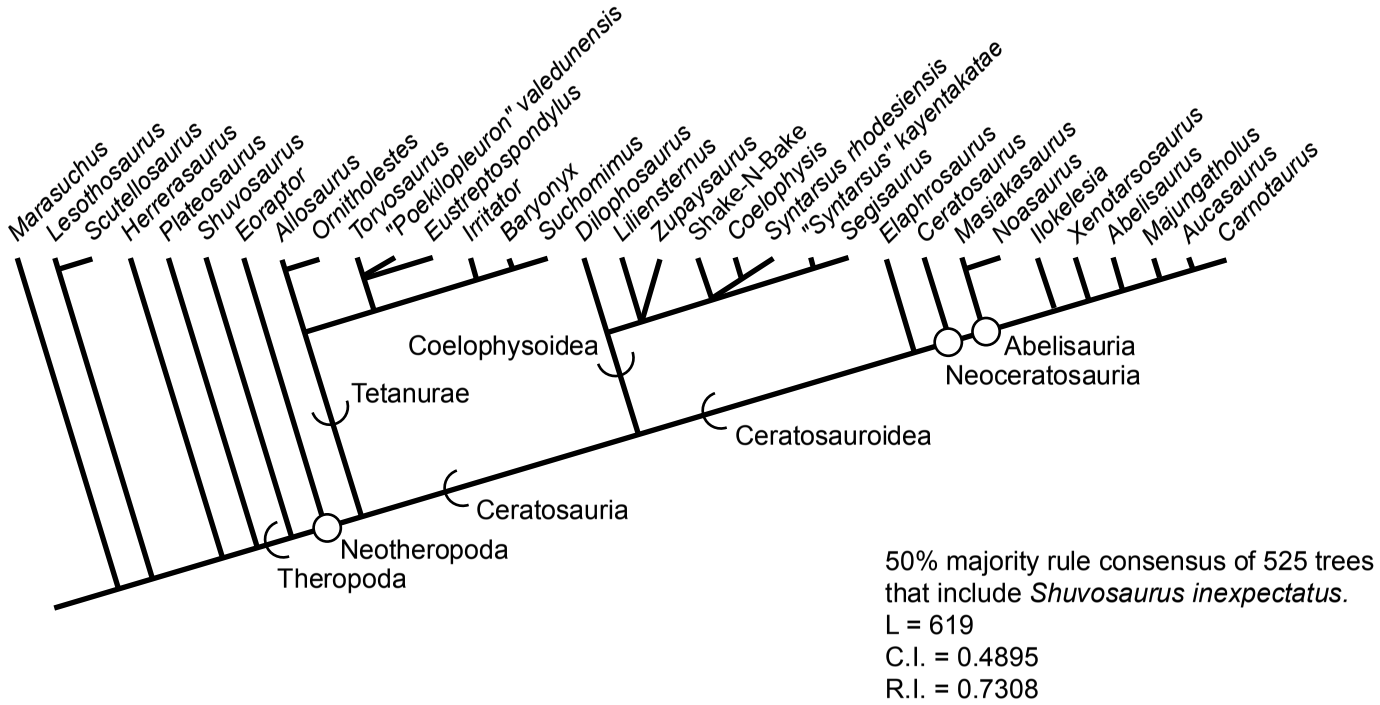


FIGURE 116C. 50% majority rule consensus tree of 525 equally most parsimonious hypotheses of basal theropod phylogeny that include *Shuvosaurus inexpectatus*. Length = 619, C.I.=0.4895, R.I.=0.7308. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

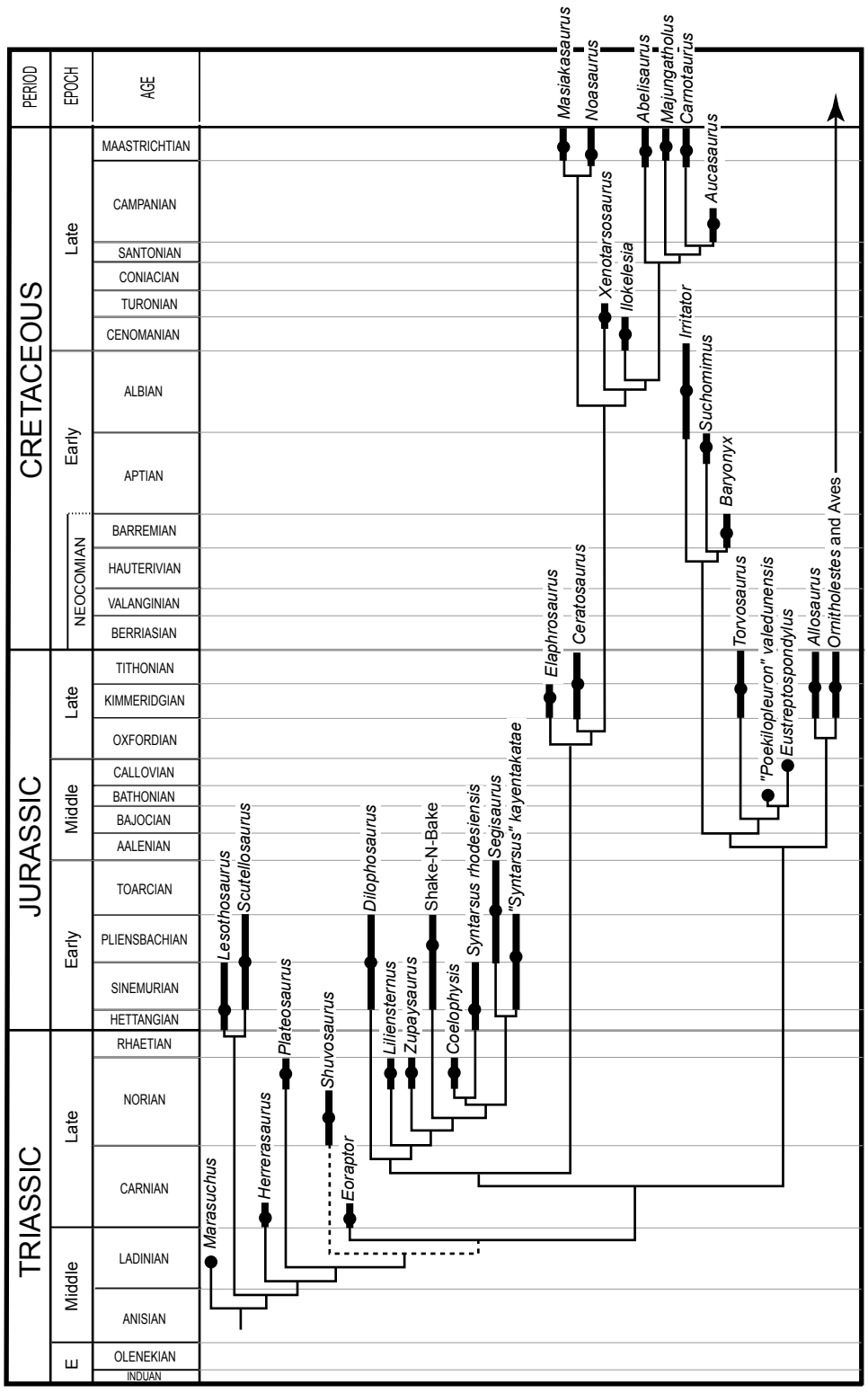


FIGURE 116D. Phylogeny based on cladogram in Figure 108D superimposed on the geologic time scale, but includes *Shuvosaurus inexpectatus*. Dashed branches indicate possible relationships for *Shuvosaurus* relative to other theropods. See text explanation of Figure 109 for further details of conventions used in this figure.

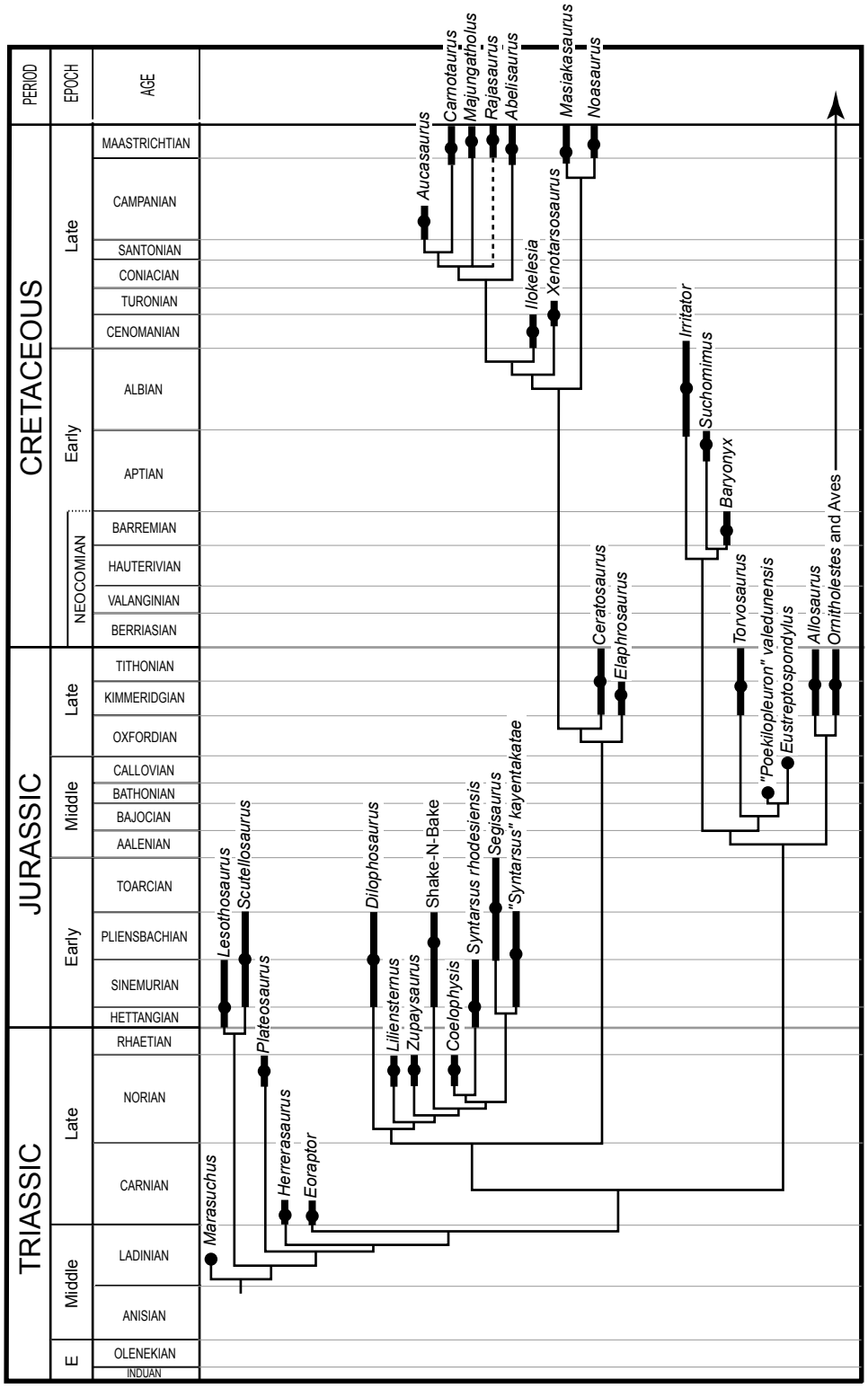
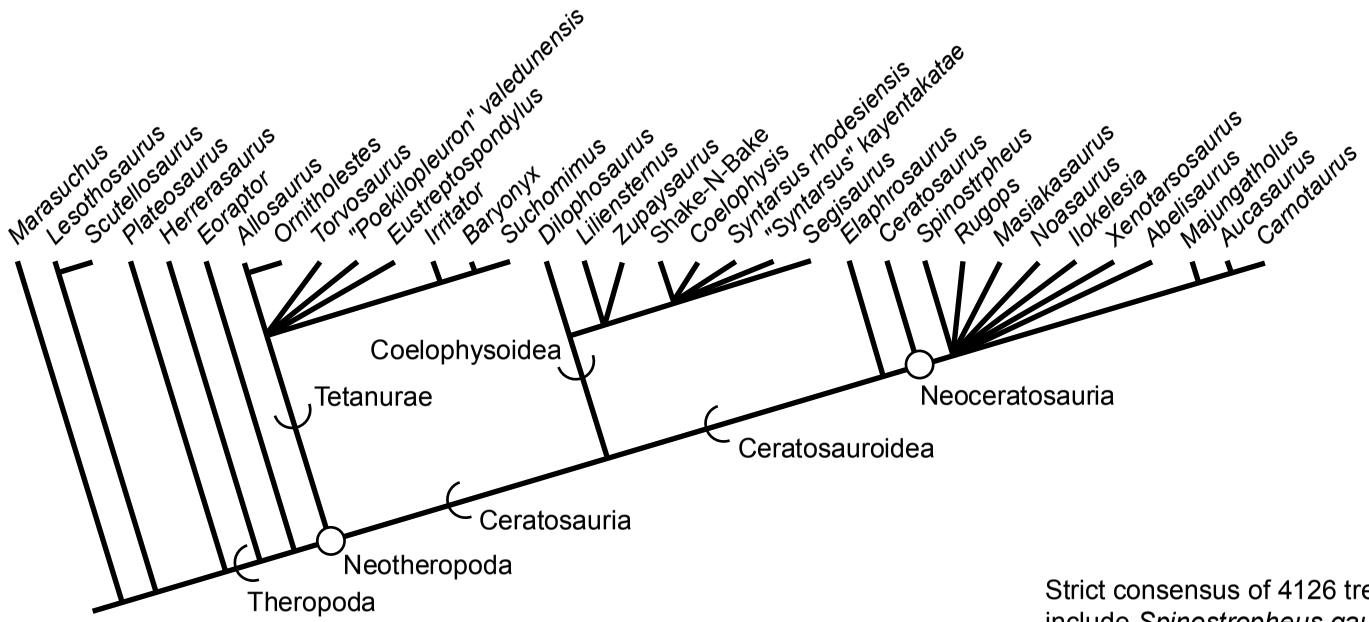


FIGURE 117. Phylogeny including *Rajasaurus narmadensis* on the geologic time scale. Dashed branches indicate possible relationships for *Rajasaurus* relative to other ceratosaurs. See text explanation of Figure 109 for further details of conventions used in this figure.



Strict consensus of 4126 trees that include *Spinostropheus gautieri* and *Rugops primus.*
L = 617
C.I. = 0.4911
R.I. = 0.7355

FIGURE 118A. Strict consensus tree of 4126 equally most parsimonious hypotheses of basal theropod phylogeny that include *Spinostropheus gautieri* and *Rugops primus*. Length=617, C.I.=0.4911, R.I.=0.7355. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

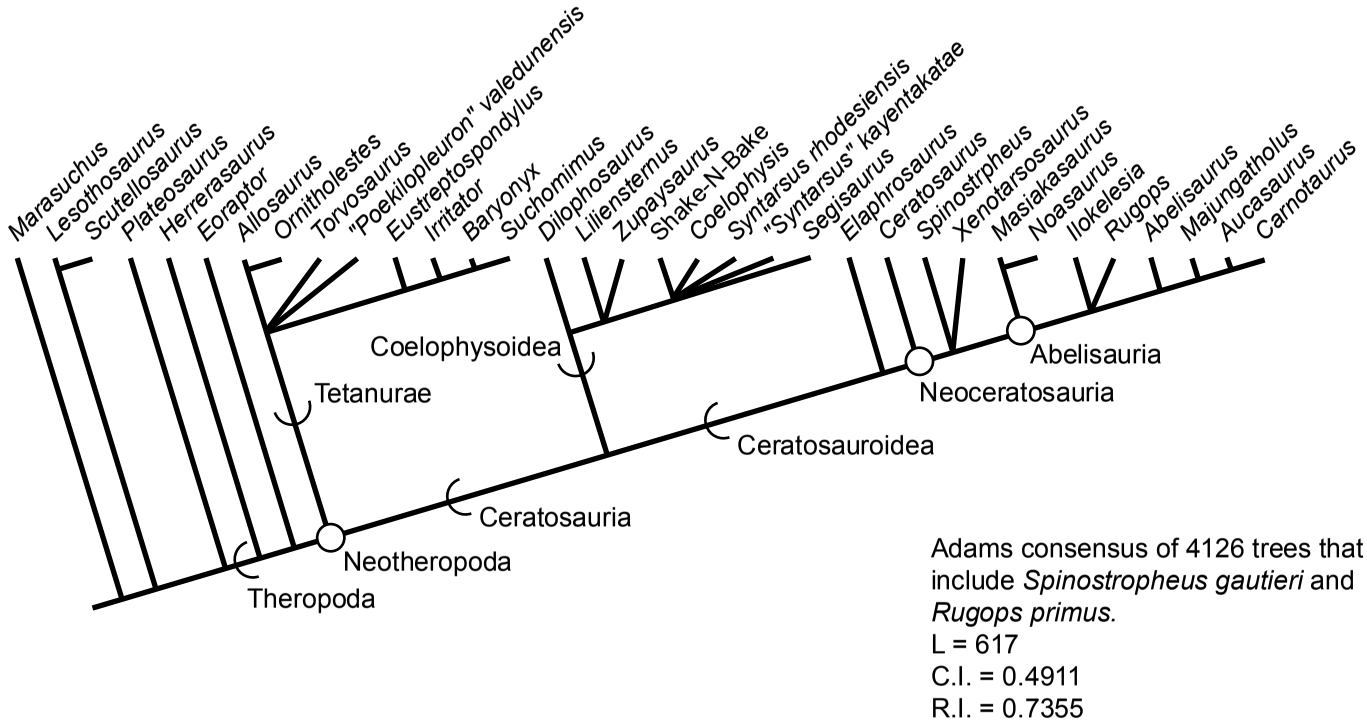


FIGURE 118B. Adams consensus tree of 4126 equally most parsimonious hypotheses of basal theropod phylogeny that include *Spinostropheus gautieri* and *Rugops primus*. Length=617, C.I.=0.4911, R.I.=0.7355. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

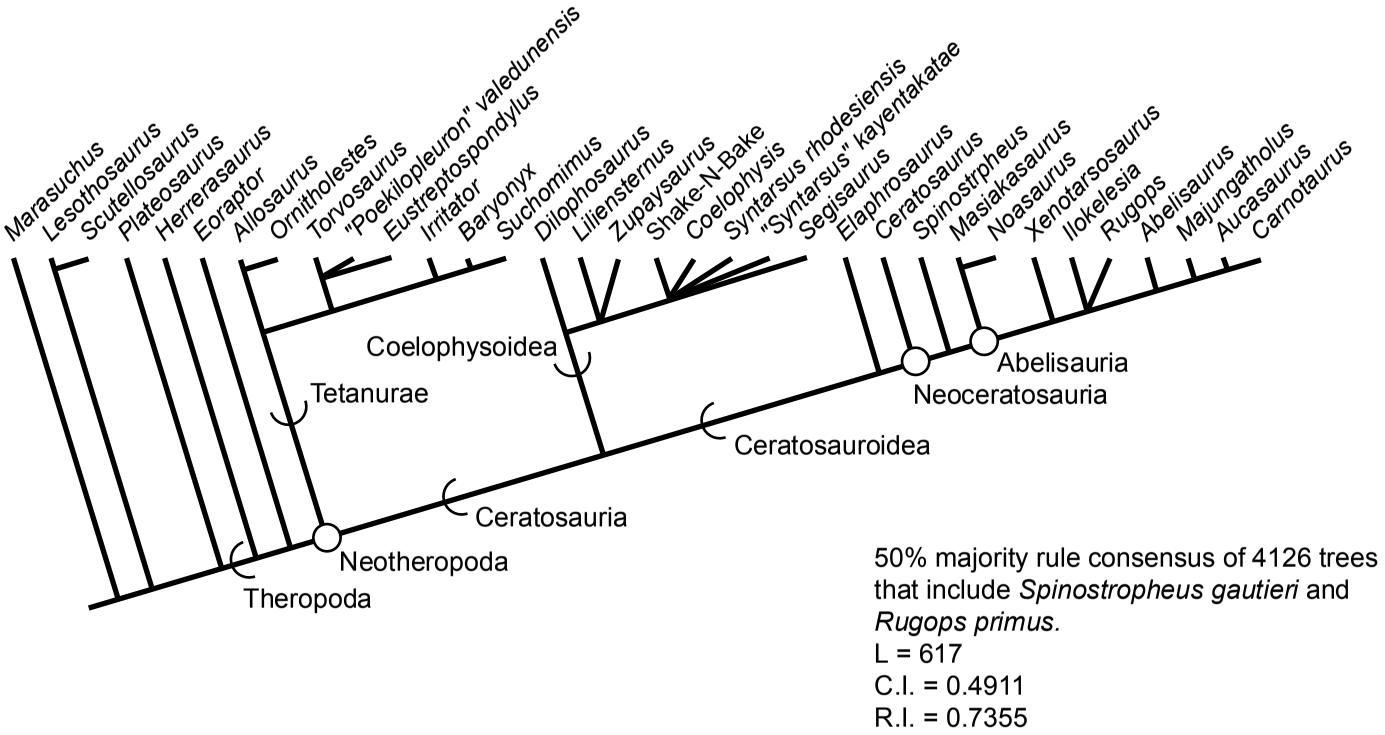


FIGURE 118C. 50% majority rule consensus tree of 4126 equally most parsimonious hypotheses of basal theropod phylogeny that include *Spinostropheus gautieri* and *Rugops primus*. Length=617, C.I.=0.4911, R.I.=0.7355. Open circles denote node-defined clade names. Arcs denote stem-defined clade names.

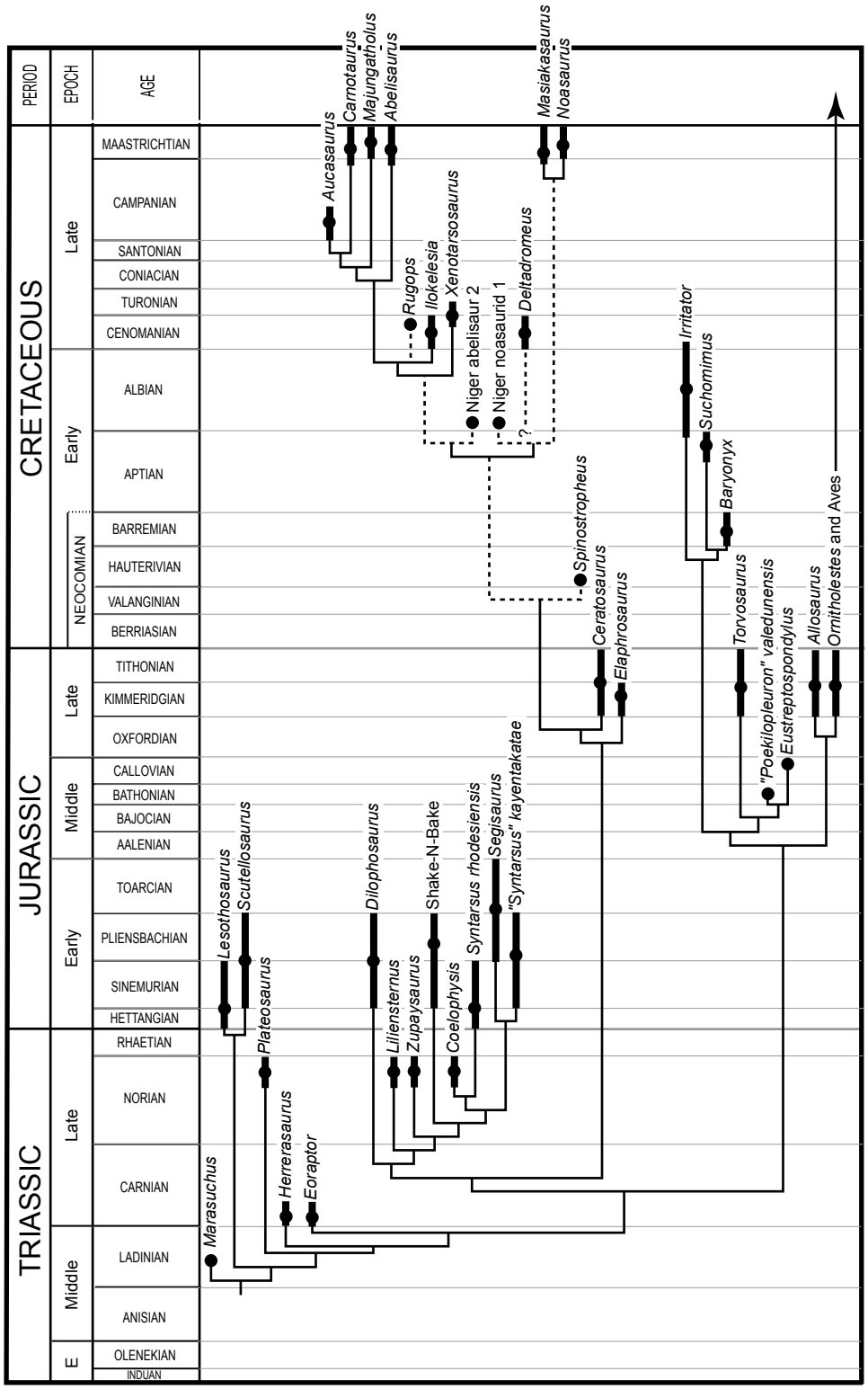


FIGURE 118D. Phylogeny including *Spinostropheus gautieri*, *Rugops primus*, two un-named abelisaur taxa (Niger noasaurid 1 and Niger abelisaur 2), and *Deltadromeus agilis* on the geologic time scale. Dashed branches indicate possible relationships for new taxa relative to other ceratosaurs. See text explanation of Figure 109 for further details of conventions used in this figure.

APPENDIX 1

Anatomical abbreviations used in text and figures.

ac = astragalocalcaneum (fused astragalus and calcaneum)
ace = acetabulum or acetabular rim
acr = acromion process of scapula
aff = astragalas fibular facet
alr = alveolar ridge
am = anterior process of maxilla
amm = anteromedial process of maxilla
apl = anterior pleurocoel
art = articular
as = astragalus
asp = ascending process of the astragalus
atc = atlantal centrum (C1)
atf = astragalus tibial facet
ati = atlantal intercentrum (C1i)
atn = atlantal neurapophysis
atr = anterior trochanter
ax = axis (C2)
axi = axial intercentrum (C2i)
bf = brevis fossa of ilium
C# = cervical vertebra
Cd = caudal vertebra
ca = calcaneum
cff = calcaneum fibular facet
cn = cnemial crest
cS = caudosacral vertebra
cstp = caudosacral transverse process
d = dentary
d# = dentary tooth
D# = dorsal vertebra
di = diapophysis
dpc = deltopectoral crest
dr = dorsal rib
dS = dorsosacral vertebra
ds1r = dorsosacral 1 rib
ds2r = dorsosacral 2 rib
ds1tp = dorsosacral 1 transverse process
ds2tp = dorsosacral 2 transverse process
dt =distal tarsal
emf = external mandibular fenestra
en = external naris
epi = epipophysis
f = frontal
fa = anterior pubic facet on pubic penducle of ilium
ff = facet for fibula
ffl = fibular flange
fh = femoral head
fi = fibula
fv = ventral pubic facet on pubic peduncle of ilium
gas = gastralia/gastralium

gl = glenoid fossa
gpm = groove for maxillary process of premaxilla
gtr = greater trochanter
hf = haemal arch facet
hg = horizontal groove on anterior face of astragalus
iaof = internal antorbital fenestra
id = interdental plates
iil = ischial peduncle of ilium
il = ilium
il.art = ilium articulation
ilat = ilial antitrochanter
ipr = infrapopliteal ridge
is = ischium
is.art = ischium articulation
isat = ischial antitrochanter
j = jugal
l. = prefix for left
la = lacrimal
lc = lateral condyle
m = maxilla
m# = maxillary tooth
maf = maxillary antorbital fossa
mc = medial condyle
mfg = medial fibular groove
mfpm = medial fossa of premaxilla (for receipt of anteromedial process of maxilla)
mpm = maxillary process of premaxilla
mt = metatarsal (numbered with Roman numerals)
n = nasal
nc = neural canal
ncr = nasal crest
od = odontoid process
of = obturator foramen
on = obturator notch
op = obturator process
orb = orbital opening
p = parietal
pap = pubic apron
pf = prefrontal
pil = pubic peduncle of ilium
pm = premaxilla
po = postorbital
poz = postzygapophysis
pozf = postzygapophyseal facet
pp = parapophysis
ppdl = paradiapophyseal lamina
ppl = posterior pleurocoel
pplf = posterior pleurocoel fossa
pplr = posterior pleurocoel recess
ppm = contact for posteroventral process of premaxilla
promf = promaxillary fenestra
promr = promaxillary recess
ps = posterior sulcus on proximal femur

pt = pterygoid
pu = pubis
pu.art = pubis articulation
pudt = pubis distal tip
puf = pubic foramen
pufn = pubic fenestra
pupl = pubic plate
pvc = pelvic canal
pvp = posteroventral process from maxillary process of premaxilla
pvfn = pelvic fenestra
q = quadrate
qj = quadratojugal
qjd = quadratojugal dorsal process
r. = prefix for right
ri = ridge
s = suture
S1 = sacral vertebra 1 (ancestral)
S2 = sacral vertebra 2 (ancestral)
s1r = sacral 1 rib
s2r = sacral 2 rib
s1tp = sacral 1 transverse process
s2tp = sacral 2 transverse process
sac = supraacetabular crest of ilium
sg = subnarial gap
sp = splenial
spf = splenial foramen
sq = squamosal
sqv = squamosal ventral process
su = surangular
sul = sulcus
sut = suture line
tfap = tibial facet for ascending process of astragalus
tfas = tibial facet for astragalus
tfc = tibiofibular crest of distal femur
ti = tibia
tp = transverse process
tpv = tibia's posteroventral process/flange
ts = trochanteric shelf
V# = vertebra

APPENDIX 2

List of ontogenetic characters used in the quantitative ontogenetic analysis conducted in Chapter 1.

1. Basisphenoid and basioccipital fusion: absent (0), or present, suture open (1), or present, suture closed (2).
2. Exoccipitals and basioccipital fusion in occipital condyle: absent (0), or present, sutures open (1), or present, sutures closed (2).
3. Supraoccipital, exoccipitals, and parietals fusion: absent (0), present, sutures open (1), present, sutures closed (2).
4. Cervical rib fusion to cervical parapophyses and diapophyses: absent (0), or present (1).
5. Vertebra 24 (V24) neural arch and centrum fusion: absent (0), present but open suture (1), present and closed suture (2).
6. Vertebra 25 (V25) neural arch and centrum fusion: absent (0), present but open suture (1), present and closed suture (2).
7. Vertebra 26 (V26) neural arch and centrum fusion: absent (0), present but open suture (1), present and closed suture (2).
8. Vertebra 27 (V27) neural arch and centrum fusion: absent (0), present but open suture (1), present and closed suture (2).
9. Vertebra 28 (V28) neural arch and centrum fusion: absent (0), present but open suture (1), present and closed suture (2).
10. Dorsosacral 2 (V24) centrum fusion to dorsosacral 1 (V25) centrum: absent (0), present but open suture (1), present and closed suture (2).
11. Dorsosacral 1 (V25) centrum fusion to sacral 1 (V26) centrum: absent (0), present but open suture (1), present and closed suture (2).
12. Sacral 1 (V26) centrum fusion to sacral 2 (V27) centrum: absent (0), present but open suture (1), present and closed suture (2).

13. Sacral 2 (V27) centrum fusion to caudosacral 1 (V28) centrum: absent (0), present but open suture (1), present and closed suture (2).
14. Dorsosacral 1 (V25) rib fusion to centrum: absent (0), present but open suture (1), present and closed suture (2).
15. Sacral rib 1 (V26) rib fusion to centrum: absent (0), present but open suture (1), present and closed suture (2).
16. Sacral rib 2 (V27) rib fusion to centrum: absent (0), present but open suture (1), present and closed suture (2).
17. Sacral (V24-V28) vertebral neural arches and neural spines fuse to one another: absent (0), or present (1).
18. Sacral transverse processes (V25-28) coalesce to form horizontal lamina: absent (0), or present (1).
19. Dorsosacral 1 through caudosacral 1 (V25-28) transverse processes fuse to ilia: absent (0), or present (1).
20. Dorsosacral 2 (V24) transverse processes fusion to ilia: absent (0), or present, suture visible (1), or present, suture obliterated (2).
21. Dorsosacral 1 (V25) ribs fusion to ilia: absent (0), or present with obvious suture (1), or present, no visible sutures (2).
22. Sacral 1 (V26) ribs fusion to ilia: absent (0), or present with obvious suture (1), or present, no visible sutures (2).
23. Sacral 2 (V27) ribs fusion to ilia: absent (0), or present with obvious suture (1), or present, no visible sutures (2).
24. Sacral ribs (dorsosacral 1 through sacral 2: V25-V27) fused to each other at distal ends: absent (0), or present (1).
25. Caudal vertebrae, anterior caudal neural arches and centra fusion: absent (0), or present with open sutures (1), or present with sutures closed (2).
26. Scapula and coracoid co-ossification: absent (0), or present with open suture (1), or present with suture closed (2).

27. Scapulocoracoid anterior margin of adults continuous and uninterrupted across scapula-coracoid contact (i.e., no notch): absent (0), or present (1).
28. Ilium-pubis co-ossification: absent (0), or present with suture open (1), or present with suture closed (2).
29. Ilium-ischium co-ossification: absent (0), or present with suture open (1), or present with suture closed (2).
30. Pubis and ischium co-ossification: absent (0), or present with suture open (1), or present with suture closed (2).
31. Pubis with distal expansion: absent (0), or present (1).
32. Ischia distal tips co-ossified: absent (0), or present (1).
33. Femur proximal surface smooth and well ossified with finished bone: absent (0), or present (1).
34. Femoral head smoothly contoured and well developed: absent (0), or present (1).
35. Femur with pronounced, projecting trochanteric shelf: absent (0), or present (1).
36. Femur with anterior trochanter a pyramidal prominence or spike: absent (0), or present (1).
37. Femur medial epicondyle a well developed crest: absent (0), or present (1).
38. Femur with infrapopliteal crest: absent (0), or present (1).
39. Femur with tibiofibular crest sharply demarcated from lateral distal condyle by sulcus or concavity: absent (0), or present (1).
40. Femur distal condyles smooth, rounded, finished surfaces: absent (0), or present (1).
41. Fibula proximal end with oblique (posteroproximal to anterodistal) ridge on medial surface that overlaps proximal part of medial fibular groove: absent (0), or present (1).
42. Fibula with medial flange that overlaps part of the ascending process of astragalus: absent (0), or present (1).
43. Astragalus ascending process suture to body of astragalus: plainly visible (0), or fully closed (1).

44. Astragalus and calcaneum fusion: absent (0), present but sutures open (1), or present, only proximal surface suture visible (2), or closed, all sutures obliterated (3).
45. Astragalus and tibia fusion: absent (0), or present with suture open (1), or present with suture obliterated (2).
46. Distal tarsal III fusion to metatarsal III: absent (0), or present with suture visible (1) or present with suture obliterated (2).
47. Metatarsal II and metatarsal III fusion of proximal ends: absent (0), or present but suture open (1), or present, suture obliterated (2).

APPENDIX 3

Ontogenetic specimen-character matrix used in Chapter 1. Taxonomic abbreviations: Dilo, *Dilophosaurus wetherilli*; Segi, *Segisaurus halli*; S.kay, *"Syntarsus" kayentakatae*; SNB, Shake-N-Bake taxon; S.rhod, *Syntarsus rhodesiensis*.

	CHARACTER			
SPECIMEN	10	20	30	40
Outgroup	0000000000	0000000000	0000000000	0000000000
Liliensternus (large)	???0??????	??????????	?????1?00?	0???0000??
Liliensternus (small)	????011??0	?010110???	000?1??000	00????????
	22	1 1		
MNA V2623 (S.kay)	2221??????	??????????	?????21???	1111111111
TMM 43688-1(S.kay)	???0222222	222222????	000????112	?111110101
UCMP 128659(S.kay)	??????????	??????????	???????000	??1100??0?
TMM 43669-3(S.kay)	??????????	??????????	??????????	??????????
UCMP 37302(Dilo)	0110?10010	000111??00	0000100000	0100000010
UCMP 37303(Dilo)	??????????	??????????	??????????	1?????????
UCMP 77270(Dilo)	2220??????	???22?1112	12?012?1??	??11111???
TMM 43646(Dilo)	??00000000	0000000000	00??000000	?100000010
UCMP 32101(Segi)	?????????1	???????????	????111111	01??11????
			2	
QG1(S.rhod)	???1222222	2222221112	222112?222	011?111?11
MCZ 9442(SNB)	????2222?1	22?2221110	1221???222	??????????
		1		
TMM 43689-4(SNB)	??????????	??????????	??????????	??????????
MCZ 9463 (SNB)	??????????	??????????	??????????	??????????

	CHARACTER
SPECIMEN	47
Outgroup	0000000
Liliensternus(large)	0012000
Liliensternus(small)	????0??
MNA V2623 (S.kay)	1112222
	3
TMM 43688-1(S.kay)	1????10
	1
UCMP 128659(S.kay)	???????
TMM 43669-3(S.kay)	??010??
UCMP 37302(Dilo)	0000000
UCMP 37303(Dilo)	??000??
UCMP 77270(Dilo)	1???0??
TMM 43646(Dilo)	00?0000
	111
UCMP 32101(Segi)	1??????
QG1(S.rhod)	1112222
	3
MCZ 9442(SNB)	???????
TMM 43689-4(SNB)	??????22
MCZ 9463(SNB)	??132??

*Note: TMM 43688-1 has both character states of character 47 preserved, and is scored as "0&1", not "0/1".

APPENDIX 4

Phylogenetic taxon-character matrix that formed the basis for the analyses in Chapter 3, and was used in unaltered form in phylogenetic test 3. Characters with two codings arranged one above the other indicate interpretation of the characters as expressing multistate polymorphism.

	CHARACTER			
Taxon	10	20	30	40
Marasuchus	??????????	??????????	??????????	??????????
Lesothosaurus	0000000100	000000000?	000?000000	000000??00
Scutellosaurus	0?????00?00	????000???	?0?????0?0	????????0?
Plateosaurus	0000000100	1000000010	0010001000	0?00000000
Herrerasaurus	0000000100	0000?00000	0001000000	101000??00
Eoraptor	0000001001	1000?0001?	0000000001	010000??01
Coelophysis	0101101010	1101011110	1001111001	0100001?01
S. rhodesiensis	0101101011	1101011110	100?111001	0100001001
"S". kayentakatae	0101101011	1101011111	0000111001	0101001003
Segisaurus	??????????	??????????	??????????	??????????
Shake-N-Bake	0?????????	??????????	????????1	0?0????????
Zupaysaurus	01111?????	?????1??10	00011?1001	010110??03
Liliensternus	0?????????	??????????	???????0?1	0?00??????
Dilophosaurus	0111100010	1101011111	0011110000	0001001102
Elaphrosaurus	??????????	??????????	??????????	??????????
Ceratosaurus	0011010000	1110100110	0011000000	0001100110
Ilokelesia	??????????	??????????	??????????	??????????
Xenotarsosaurus	??????????	??????????	??????????	??????????
Aucasaurus	1011?1??0?	1?1??001?0	21??00?0??	10?1000???
Abelisaurus	101?110?00	1?10?00??0	2111??00?0	1011100??20
Carnotaurus	1011010100	1110?00110	2101000000	1011100??20
Majungatholus	1011010?00	1110100?10	2111000000	1011000120
Masiakasaurus	0?????????	???????010	2??1?101?0	0000100???
Noasaurus	0?????????	????????10	2?00??01?0	?0?00000??
Torvosaurus	0011000000	1?10?00?11	0021000000	00001001??
Baryonyx	01???00110	11?0000011?	????11?0?0	?0?????110
Irritator	01110?????	11??????10	102????010	100200??10
Suchomimus	0111000110	1100000110	0021111010	1?02002?10
"*P.*" *valedunensis*	0??1100?00	1??00???11	0021??0010	0102100?0?
Eustreptospondylus	0?????00?00	11?0000?11	??21?0????	?0?210?1??
Allosaurus	0011000100	1000000010	0011000010	0002010101
Ornitholestes	0000000?00	1000?00110	00?1000110	000201??00

Taxon	50	60	70	80
Marasuchus	??????????	??????????	??????????	???????000
Leosthosaurus	0000000000	0000100?10	0000000?00	0000000000
Scutellosaurus	00????????	??????????	??????????	??????????
Plateosaurus	0011000000	0010000000	0000000010	0000000000
Herrerasaurus	0000000000	0000000000	0000000001	11000?0000
Eoraptor	0001000?00	0110000010	0000001021	1?0?000?00
Coelophysis	0011100000	0110200010	0000000022	10000?0?1?
S. rhodesiensis	0011100000	0110200010	000000002?	1000000111
"S". kayentakatae	0011100000	0110200110	?000000012	1000000111
Segisaurus	??????????	??????????	??????????	??????????
Shake-N-Bake	??????????	??????????	??????????	??????????
Zupaysaurus	001?100000	0110201110	0?0000?002	01110?0???
Liliensternus	??????????	??????????	??000?????	01???0????
Dilophosaurus	0011100??0	0110000110	00000?0102	01??000110
Elaphrosaurus	??????????	??????????	??????????	??????????
Ceratosaurus	0021100000	0110001111	0000011022	0101111110
Ilokelesia	??????????	?????1????	?0100?????	???0??????
Xenotarsosaurus	??????????	??????????	??????????	??????????
Aucasaurus	???1??21??	?1111??0?0	??????????	????1?????
Abelisaurus	1121010101	111??10?00	1110??????	?121111??
Carnotaurus	1121012111	1111110000	1110111101	0121111117
Majungatholus	1121011111	1111110000	1110111101	012?11111?
Masiakasaurus	??????????	??????????	??????????	??????????
Noasaurus	??????????	??????????	??????????	?????1????
Torvosaurus	??????????	?111001011	000101?0?2	0??0?1????
Baryonyx	0???000000	0111101011	0?000??0??	1??0?20110
Irritator	0010000000	0111001011	0100010012	11?00??110
Suchomimus	0010000000	011110??1?	0?????????	????2?????
"P". valedunensis	????100000	0111000010	000101?0??	01?0??0???
Eustreptospondylus	????0?????	?11??01?11	???1?1????	?1?????11?
Allosaurus	0111000000	0110001011	0000010112	0110002110
Ornitholestes	001???0000	011???101?	0??0?0?0?1	0010002???

Taxon	90	100	110	120
Marasuchus	0?????????	??????????	?00?00??00	0000000010
Leosthosaurus	0000000000	0000020000	0000000000	000011?0?0
Scutellosaurus	??????000?0	?????0?000	?00?000000	000???????
Plateosaurus	0000000010	1000001000	0000000011	0000000000
Herrerasaurus	?000?00000	0?00000?0	0000000?11	0000000000
Eoraptor	?????????0	???0?000???	000?000??1	000???0???
Coelophysis	?000?110?0	??00111???	?01?111012	0000110110
S. rhodesiensis	0000111?0?0	??00111000	10??111?12	0000110110
"S". kayentakatae	010?110010	1?10111???	10??111012	0000110110
Segisaurus	??????????	??????????	??????????	??????????
Shake-N-Bake	??????????	??????????	?011111?1?	000???????
Zupaysaurus	?????00000	??1???????	??????????	??????????
Liliensternus	????1110?0	???????000	1000101?1?	000???????
Dilophosaurus	?00??10000	??001?0?0?	1011111012	0000111110
Elaphrosaurus	??????????	??????????	?001111?11	000???????
Ceratosaurus	?111000?0	110?020100	0010112213	0001000111
Ilokelesia	??????????	??????????	?01?112013	011???????
Xenotarsosaurus	??????????	??????????	??1?11??13	??????????
Aucasaurus	??????????	??0???????	?????????3	111???????
Abelisaurus	??1???????	???????110	??????????	??????????
Carnotaurus	?11??00111	1?01020110	0011112213	1111000111
Majungatholus	0111000111	1101020110	0011112213	011100????
Masiakasaurus	?????00111	00?????101	101?002113	011???????
			11	
Noasaurus	??????????	???????10?	??????????	1?1???????
Torvosaurus	?????0????	????000100	0111102113	000???????
Baryonyx	?1???11000	11??111001	1111102?13	0001001000
Irritator	?1????????	??????????	??????????	??????????
Suchomimus	?????11?00	?????1????	11???????1?	??????????
"P". valedunensis	10???0????	10????????	0?????????	??????????
Eustreptospondylus	110??00?0?	????000001	1111102113	0?00?011??
Allosaurus	1101200000	1001020100	0110102113	0001001001
Ornitholestes	?1??200000	1??11?0???	0111102?13	000???????

Taxon	130	140	150	160
Marasuchus	0000000000	????000?00	1000000000	00000?0000
Leosthosaurus	0001000000	????000000	000??11000	0?00000000?
Scutellosaurus	?000000000	????000000	0000?11000	000000?0?0
Plateosaurus	0010000000	0000000100	0000001000	0000000000
Herrerasaurus	0000000000	????000100	0010000000	00100?0120
Eoraptor	?01000000?	?000000?00	000001?00?	????0????0
Coelophysis	0010012101	1?00010111	1100111001	1111000100
S. rhodesiensis	0010012101	11000?0111	1100111001	1111000110
"S". kayentakatae	0010012101	11?0?101??	???0111001	1??1??0???
Segisaurus	??????????	1???????11	??????????	????000??0
Shake-N-Bake	0010012201	1???010111	11?0111001	11110001??
Zupaysaurus	??1?????01	??????????	?????????1	??????????
Liliensternus	00100?000?	??00010111	10?????00?	????0?0???
Dilophosaurus	0000000000	??00010111	1010111001	1111010110
Elaphrosaurus	1010000201	????000111	1001111101	1110000?1?
Ceratosaurus	0000000001	??10001111	0011111111	1111001100
Ilokelesia	?111111000	??111?1?0?	00????????	???110???0
Xenotarsosaurus	???????0??	?????1????	??????????	??????????
Aucasaurus	??11??????	??????????	??????????	????110??0
Abelisaurus	??????????	??????????	??????????	??????????
Carnotaurus	1111111000	1011111101	0011111111	10??111???
Majungatholus	1111111000	??11??11??	001?11111?	1???001??0
Masiakasaurus	?011111010	??1110?1??	11?????001	1???00011?
Noasaurus	?0111???10	??11??????	11????????	??????????
Torvosaurus	0000000000	????010100	001???????	??00000??0
Baryonyx	0000000000	?010010100	001???????	?????????0
Irritator	??????????	??????????	??????????	??????????
Suchomimus	?????????0	0??0???1??	?01???????	??0???????
"P". valedunensis	??????????	??????????	??????????	??????????
Eustreptospondylus	10?00??00?	?????10100	101????0??	?????0?0???
Allosaurus	0000000000	0010010100	0010111000	0000000221
Ornitholestes	10000??000	??????0100	11?0111?0	0?0?0??221

Taxon	170	180	190	200
Marasuchus	0?0??0??00	000?00????	????????00	0000000001
Leosthosaurus	??00000?00	0000000000	0000000001	0100000000
	1			
Scutellosaurus	0?0100?000	000000?0??	????????01	1100001000
Plateosaurus	0000000000	0101000000	1010000000	0000000000
Herrerasaurus	??0010??00	0000000100	0101011100	0000000000
Eoraptor	00000??000	0100000100	1001011100	00100?10?0
Coelophysis	010010?000	0100001100	1111111210	1110111110
S. rhodesiensis	110010?000	0100001100	1111111210	1110111110
"S". kayentakatae	?100111000	???0???1??	?????10?10	?11?111110
Segisaurus	?11011?00?	010??0????	????????1?	????1?????
Shake-N-Bake	???????0??	??????????	????????10	?11?111010
Zupaysaurus	??????????	??????????	??????????	??????????
Liliensternus	???010?000	010000?1??	?????????0	1110111100
Dilophosaurus	1?001??000	0100001100	111?111210	1110111000
Elaphrosaurus	??0????101	1112?0?1??	??????????	111?111101
Ceratosaurus	1?01011000	1000???100	1????1?211	0111011?01
Ilokelesia	0?????????	??????????	??????????	??????????
Xenotarsosaurus	??????????	??????????	??????????	??????????
Aucasaurus	10011??1?1	1102110010	000??112?1	11110?11?1
Abelisaurus	??????????	??????????	??????????	??????????
Carnotaurus	0?01111111	101211?01?	00????1211	1111011101
Majungatholus	1?01???111	1012??????	?????????1	1111011101
Masiakasaurus	?????????1	1??2??????	????????0?	??????????
Noasaurus	??????????	??????????	??????????	??????????
Torvosaurus	1????????0	110110?101	1?1??2120?	0111001001
Baryonyx	0?0?0??1?0	110110????	??1??????0?	0???0010?1
Irritator	??????????	??????????	??????????	??????????
Suchomimus	?100000100	??0110?10?	1???????00	0011?010?1
"P". valedunensis	??????????	??????????	??????????	??????????
Eustreptospondylus	???1??????	0?01??????	??????????	01????1001
Allosaurus	2111000100	0100001101	1111121201	0111001001
Ornitholestes	2??????0?00	010?00??01	1??1121201	0111001001

Taxon	210	220	230	240
Marasuchus	0000001000	0001000000	?000?00?00	000000?000
Leosthosaurus	0000010010	0000000000	0210000000	0001000000
Scutellosaurus	0000210010	00000?0000	02000?000?	0001000001
Plateosaurus	0000000000	0000001000	0000000000	0000000000
Herrerasaurus	0000000002	0000000000	0000000000	0000000010
Eoraptor	0000101000	00000?100?	??0??00?0?	?0?0010??0
Coelophysis	0010111111	0111011001	1100111101	1011111111
S. rhodesiensis	0010111110	0?11011001	1101111?01	1011111111
			2	
"S". kayentakatae	0010?11111	0011??1001	?10?111101	1011111111
Segisaurus	????11111?	00?10?0???	?10??1??0?	?011??112?
Shake-N-Bake	001?111???	???10???01	11011?1101	10111111??
			2	
Zupaysaurus	??????????	??????????	????1?????	????11????
Liliensternus	0010?11111	01110?1001	?10?0?0?01	101?11??10
Dilophosaurus	0010111111	01?1012001	11011?1?01	1011111111
Elaphrosaurus	0001?1????	????002001	?20111??01	101?02??1?
Ceratosaurus	0001111002	??01012001	1200111111	1011121121
Ilokelesia	??????????	??????????	??????????	??????????
Xenotarsosaurus	??????????	???????001	?200211111	101?121?2?
Aucasaurus	??????0??2	1?0????2???	?20?????11	?1?11???21
Abelisaurus	??????????	??????????	??????????	??????????
Carnotaurus	000?110102	1100012000	?201211?1	1?1???102?
Majungatholus	0001??????	????????0??	?201??????	?11??2102?
Masiakasaurus	???1111001	1??????001	1211211011	101112????
Noasaurus	??????????	??????????	??????????	??????????
Torvosaurus	0100000101	0100001???	????????01	102?121011
Baryonyx	0100?1?10?	01?001??11	????0000?1	??????1011
Irritator	??????????	??????????	??????????	??????????
Suchomimus	?10??10???	?????111??	?????0????	?0????1???
"P". valedunensis	??????????	??????????	??????????	??????????
Eustreptospondylus	0?002?0??2	010????111	?211110??1	102?12001?
Allosaurus	1100210102	0100111111	0211110001	1021121011
Ornitholestes	1000110???	??00100111	?2111?0???	??????101?

Taxon	250	260	264
Marasuchus	0000000000	0000000000	1000
Leosthosaurus	00?????0??0	1000000000	??00
Scutellosaurus	0000100000	?0?0000000	??0?
Plateosaurus	0000010000	0000000000	0000
Herrerasaurus	0000010000	0000000000	0000
Eoraptor	????0?????	??0000?000	1000
Coelophysis	1000110111	01111?10?1	1000
S. rhodesiensis	1020110?11	1111111011	1000
"S". kayentakatae	1020110111	1111111001	1100
Segisaurus	??????????	???1???0??	100?
Shake-N-Bake	1020110111	111??110??	????
Zupaysaurus	0010110110	??????????	????
Liliensternus	0?0011001?	0??????001	??0?
Dilophosaurus	?011110l?0	1?1111?000	1100
Elaphrosaurus	????1???10	10????0111	????
Ceratosaurus	1020111111	201???0011	??0?
Ilokelesia	??????????	??????????	??11
Xenotarsosaurus	?111111111	2??????????	????
Aucasaurus	?01?1???11	?011110?1	10??
Abelisaurus	??????????	??????????	????
Carnotaurus	??????????	??????????	????
Majungatholus	?11111111?	???????0?1	??11
Masiakasaurus	0111111111	2?????01??	??1?
Noasaurus	??????????	???????1??	????
Torvosaurus	0020111100	20????0000	????
Baryonyx	????????0?	2??????????	????
Irritator	??????????	????????0?	????
Suchomimus	??????????	????????0?	????
"P". valedunensis	??????????	??????????	????
Eustreptospondylus	?0211111??	2??????000	??0?
Allosaurus	0021111100	2011110000	1100
Ornitholestes	00????????0	???????000	????

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